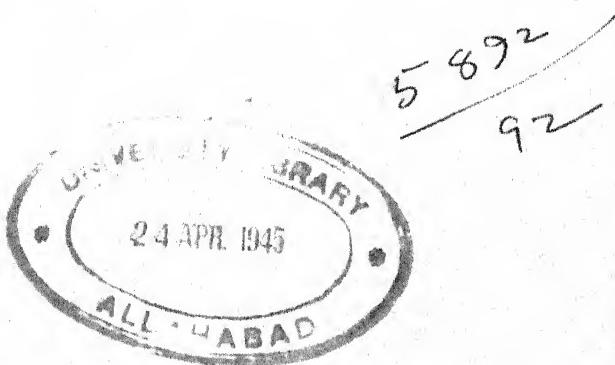


AQUATIC PHYCOMYCETES
EXCLUSIVE OF THE SAPROLEGNIACEAE
AND PYTHIUM

By

FREDERICK K. SPARROW, JR.



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To

NAN GABLER SPARROW

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PREFACE

IN THE more than two and one-half decades which have ensued since the completion of publication of Minden's treatment of the lower, primarily aquatic, groups of Phycomycetes in *Kryptogamenflora der Mark Brandenburg* considerable new material has been accumulated about these curious and oftentimes very unplantlike organisms. The later researches, added to those of the earlier period of activity, which might well be considered to have terminated with Minden's contributions to the field, have resulted in the bringing to light of a rather rich and certainly a remarkably diverse flora composed of a hitherto unsuspected number of species. New types of sexuality and life histories have been discovered, and much has been learned of the nuclear phenomena; methods of cultivation have been evolved and other material of general biological interest made available. Coker (1923) has provided an invaluable aid to the student of the Saprolegniaceae in his monograph of that family. Furthermore, the aquatic as well as the amphibious and terrestrial species of the important genus *Pythium* have been dealt with in recent years by Miss Matthews (1931). Since the authoritative monographs of Coker and Miss Matthews are in English and of relatively late date and, in addition, since they deal with well-defined compact groups the reader is referred directly to them. There remains, however, a not inconsiderable number of organisms that have not been touched upon by either of these authors or by students of special groups (Kanouse, 1927; Indoh, 1940; and others), including in particular the large and notoriously difficult order of the Chytridiales.

The present volume is intended to give an account of the Phycomycetes, other than the Saprolegniaceae and *Pythium*, that occur in fresh and marine waters. Any biological treatise that attempts to circumscribe organisms primarily on the basis of their habitat inevitably encounters difficulties. These have not been overcome here. In general, groups whose members are predominantly inhabitants of terrestrial host plants, for example *Synchytrium* and *Physoderma*, are not dealt with, although it is evident from their structure, reproduction, and development that they might conceivably be regarded as aquatic fungi adapted for entering and occupying a

special type of habitat, the living cytoplasm of their phanerogamic hosts.

It is inevitable that a book requiring some years of preparation, as this one has, should suffer to a degree from lack of uniformity, due oftentimes to a changing point of view on the part of the author. An attempt has been made, however, to be consistent in most matters, particularly in the diagnoses of genera and species. Although the classification departs from that generally used, it is believed that the taxonomic treatment is essentially a conservative one. If any doubt exists as to the distinctiveness of a species, it has not been placed in synonymy. This seems a justifiable course considering the relatively few accounts thus far published of most of these fungi and, in many groups, our as yet primitive methods of studying them. If a suitable English diagnosis is available, it has been quoted directly. Occasionally such diagnoses have been slightly modified in the interests of conciseness or in order to include additional pertinent information. Unless a specific description is accompanied by citation of a collection made by me, it has been compiled. After each specific description the substrata, collectors, and place of collection are given, together with the citation of accounts and figures in the literature. A question mark preceding the name of the substratum indicates doubt as to the identity of the *fungus*; a question mark after this name implies doubt as to the identity of the *substratum*. Needless to say, precision in the citation of "countries" has sometimes suffered from events of the times. Austria, Czechoslovakia, and East Prussia are here included under "Germany." Scherffel's collections made largely before the first World War are given simply as in "Hungary." When matters of international suzerainty become more static than at present, these locality names can be amended. Species considered imperfectly known are preceded by a question mark, those rejected, by an asterisk. Very recent material is interpolated wherever possible. The figures should be considered in conjunction with the text to which they apply and which they are intended to supplement.

A few specimens are cited; the following abbreviations denote the location of the material:

- B. M. British Museum (N. H.), London
- F. Farlow Herbarium, Harvard University
- L. Herbarium of D. H. Linder, Harvard University
- S. Sparrow collection

It is probable that no book of this nature ever appears without the friendly support and active coöperation of various persons and institutions. Particularly is this true of the present work in all its phases.

The preparation of the manuscript was immeasurably facilitated by grants from the Faculty Research Fund and the Horace H. Rackham Fund. Its publication was made possible by appropriations by the Board of Regents of the University of Michigan.

The laborious task of preparing reproductions of illustrations from other authors has for the most part been done by Richard Higgins and Frances Gracey. Permission to use these illustrations has been generously given wherever the authors could be reached; the sources have been acknowledged in each instance. Professor H. Munro Fox, editor of *Biological Reviews*, has kindly allowed the reproduction of Figure 1, which is taken from that journal. James McCranie has generously contributed certain figures on the cytology of *Allomyces*, and V. M. Cutter, Jr., that of *Rozella Allomycis*. If no acknowledgment is made, the illustration is an original one prepared for this book. I am indebted to Professor Sarah Bach-Wiig, of Smith College, for the portrait of Dangeard, to the botany department of Michigan State College for that of Zopf, and to Doctor O. Gram, of Copenhagen, for that of Petersen.

To Miss Grace Potter, assistant editor of scholarly publications of the University of Michigan, I should like to express my very great appreciation for her painstaking editing and careful supervision of the manuscript while in the process of publication. To Nan Gabler Sparrow, I am greatly indebted for help in reading proof and for her ready and able assistance in the preparing of this and other manuscripts for publication.

Because of the almost total lack of herbarium specimens of aquatic Phycomycetes and the paucity of significant data to be derived from such specimens as are available, the would-be monographer of these fungi has, perforce, to seek out his material in nature and to study it in the laboratory in the living state. That a large number of aquatic Phycomycetes have been so studied in preparation for this book has been made possible to a considerable degree by the tenure of National Research Council fellowships in the Biological Sciences and by the hospitality of the directors of many laboratories and institutions. It is a pleasure at this time to express my appreciation to Professor L. M. Massey, chairman, and H. H. Whetzel, acting

chairman, of the Department of Plant Pathology, Cornell University; the late Professor Sir Albert Seward, formerly professor of botany, The Botany School, Cambridge University; Professor Knud Jessen, director of the Planteanatomiske Laboratorium, University of Copenhagen; the director of the Universitetets Havbiologiske Laboratorium, Fredrikshavn, Jutland; Sir Edwin Butler, F.R.S., sometime director of the Imperial Mycological Institute, Kew; John Ramsbottom, F.L.S., Keeper of Botany, the British Museum (N. H.); the late Doctor Reginald Harris, formerly director of the Cold Spring Harbor Biological Laboratory; Professor H. B. Bigelow, lately director of the Woods Hole Oceanographic Institution. I am greatly indebted to my colleagues, Professors H. H. Bartlett, chairman of the Department of Botany, W. R. Taylor, and L. E. Wehmeyer, for advice solicited from time to time. D. H. Linder, S. A. Waksman, H. M. Fitzpatrick, and Ralph Emerson have all contributed in one way or another to the furtherance of this volume. Miss Hilda Harris, librarian of the Farlow Library, Harvard University, and Miss A. C. Atwood, botanical bibliographer of the Bureau of Plant Industry, have been of the greatest assistance in bibliographical matters.

I am deeply indebted to Professor E. B. Mains, director of the University of Michigan Herbarium, for his painstaking reading of the entire manuscript, for valuable suggestions, and for helpful criticism and advice. Professor J. N. Couch, of the University of North Carolina, kindly read critically the introductory material of the orders and made certain suggestions.

My sincere appreciation is expressed at this time to F. T. Brooks, F.R.S., professor of botany, Cambridge University, and to Docent Doctor H. E. Petersen, of the University of Copenhagen, for their active sponsorship of my researches and their continuing interest.

Finally, it is a genuine pleasure to acknowledge my great and lasting indebtedness to Professor W. H. Weston, Jr., of Harvard University, who, by his stimulating guidance and his love for and profound knowledge of aquatic Phycomycetes, first aroused my interest in these most curious organisms.

F. K. S., JR.

ANN ARBOR, MICHIGAN

December, 1940

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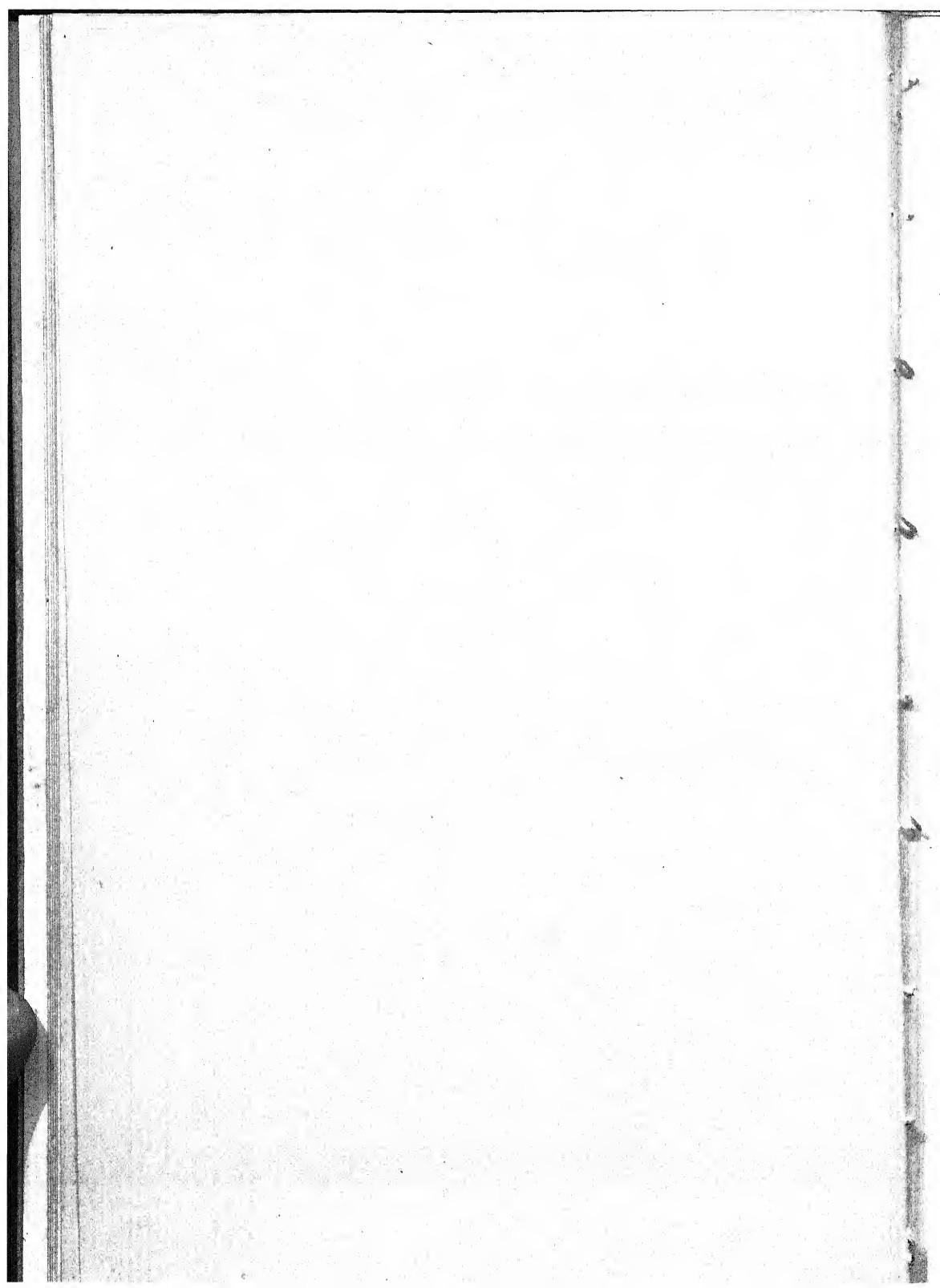
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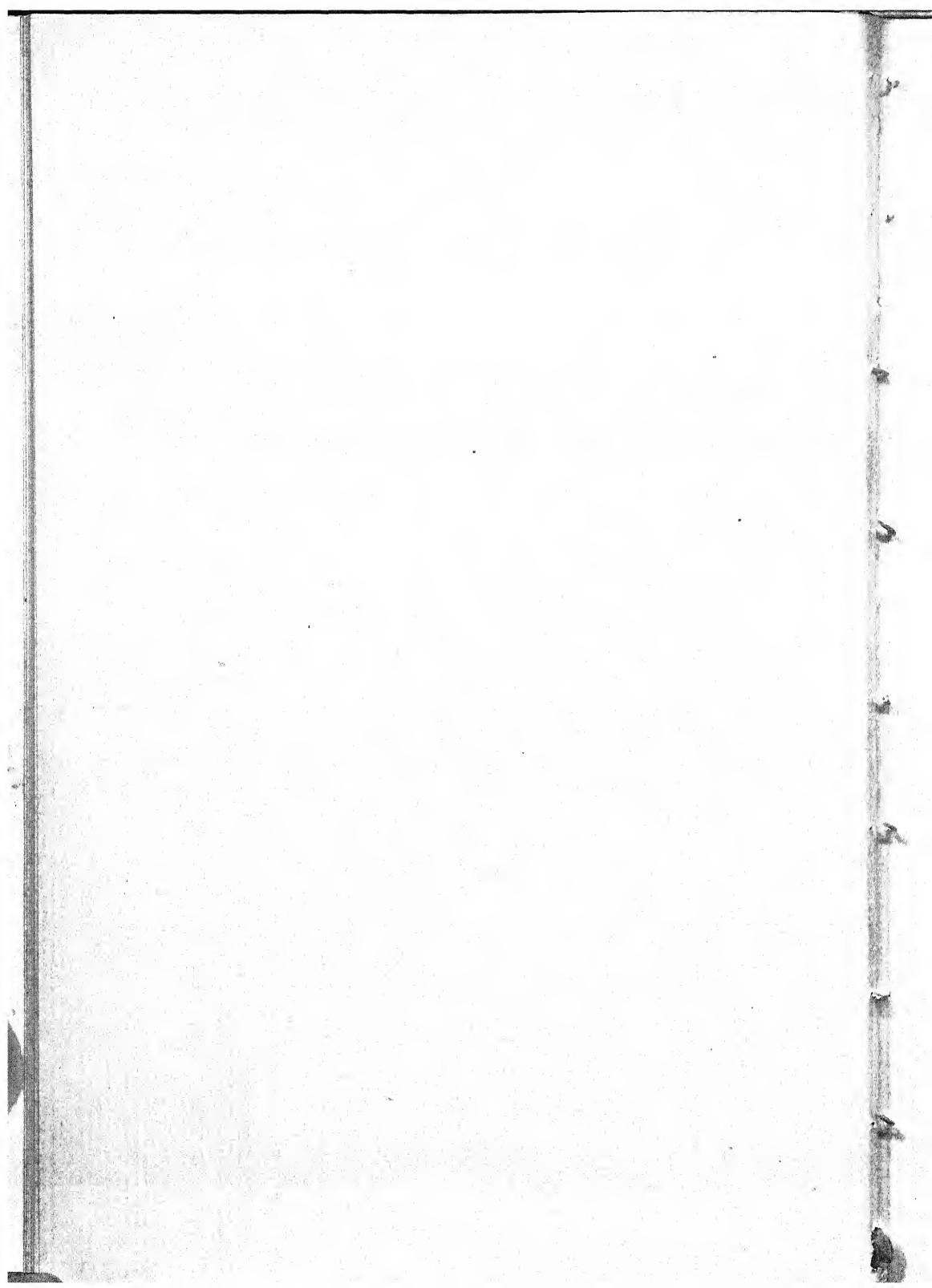
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INTRODUCTION

ANY truly comprehensive account of the interrelated and delicately balanced society of plants and animals existing in waters should consider all the entities, great and small, which form a part of it. As is well known, green plants by their photosynthetic activities add new materials in organic form to their environment and hence contribute in a positive way to this society. Organisms lacking chlorophyll must, for the most part, depend ultimately upon the synthesizers for their existence. Yet such nonproducers are not to be regarded as mere impoverishers of the food supply, for they may perform useful and, indeed, necessary functions in the reduction, reworking, and transformation of organic materials, and, as Bigelow (1931) in referring to the activities of marine bacteria has well put it, in the keeping in "... action of the cycle of matter through its organic and inorganic stages."¹ By far the greatest number of plants lacking chlorophyll belong in the fungi, a group which, though primarily terrestrial, has a number of aquatic representatives. These are for the most part Phycomycetes ("algal fungi") although the Myxomycetes, Ascomycetes, and Fungi Imperfecti all contain truly aquatic species.

The Phycomycetes are ordinarily considered the most primitive of the true fungi. As a group, they include a wide diversity of forms, some showing definite relationships to the flagellates, others closely resembling colorless algae, and still others being true molds. The vegetative body (*thallus*) may be unspecialized and converted as a whole into a reproductive organ, or bear tapering rhizoids, or be mycelial and very extensive. In any event, its outstanding characteristic is a tendency to be nonseptate and, in most groups, multinucleate, cross walls being laid down in vigorously growing material only to delimit the reproductive organs. The unit of nonsexual reproduction, the spore, is borne in a sporangium, and, in the aquatic and semiaquatic orders, is provided with a single posterior flagellum, or a single anterior one, or two laterally or terminally attached ones.

¹ For accounts of the significance of aquatic fungi from a limnological standpoint see Welch (1935) and, particularly, Weston (1941).

Sexual reproduction is accomplished in one great group, the "Zygomycetes," by the well-known process of conjugation of the tips of two mycelial branches, which results in the formation of a thick-walled zygosporc; only nonmotile spores are formed. In the other orders, generally spoken of collectively as the "Oomycetes" (to which many students assign the forms treated in the present work), there is great diversity in the method of sexual reproduction, and, as in the green algae, all gradations from isogamous planogametic to oögamous aplanogametic types occur. Nor is the character of the sexual reproduction necessarily linked with the degree of thallus development. Thus planogametes (isogamous) are found in the endobiotic holocarpic genus *Olpidium*, a form with a simple thallus, and planogametes (anisogamous) likewise occur in *Allomyces*, a eucarpic form with a well-developed mycelium. On the other hand, in *Sapromyces*, a member of the Leptomitales, though the thallus resembles that of *Allomyces* sexual reproduction is by oögamy of a high type and, in general, involves, as in the better-known genera *Saprolegnia* and *Achlya*, the formation of an oöosphere contained in an oögonium and of an antheridium; fertilization is accomplished by the transference of antheridial material into the oögonium through a specialized tube produced by the male gametangium. A single thick-walled oöspore is formed from the fertilized egg. This type of sexual reproduction is characteristic of the higher aquatic and semi-aquatic orders. Other variations occur, but these are sufficient to illustrate the diversity found in the Oomycetes.

The Phycomycetes comprise the following orders:¹

Chytridiales	}	Zoosporic, aquatic series
Blastocladiales		
Monoblepharidales		
Plasmodiophorales		
Saprolegniales		
Leptomitales		
Lagenidiales		
Peronosporales (primarily terrestrial, except for the family Pythiaceae, which is amphibious)		
Mucorales	}	Conidial, terrestrial series
Entomophthorales		

¹ This grouping of the orders of the Phycomycetes was for the most part suggested by Professor W. H. Weston, Jr., of Harvard University.

The aquatic series is here regarded as composed of the fungi which are found on various plant and animal substrata in water or in damp soil. In this field, as elsewhere in biology, no hard and fast distinction can be drawn between aquatic, amphibious, and terrestrial organisms. The present volume, however, deals with no groups the great majority of whose members inhabit terrestrial phanerogams.

PHYLOGENY AND RELATIONSHIPS

The relationships and particularly the phylogeny of the fungi to be described here have always had a peculiar fascination for the speculative mycologist. Lengthy accounts have appeared almost since the beginning of the investigations on aquatic Phycomycetes, purporting to show beyond question that these fungi are derived from algae by loss of chlorophyll, or from higher fungi by the degenerative effects of parasitism, or from simpler flagellate or monad ancestry (for a full discussion in English of these theories see Atkinson, 1909b; Petersen, 1910; Cavers, 1915; Cook, 1928; Gaumann and Dodge, 1928; Fitzpatrick, 1930). As might be expected of any discussions on the phylogeny of organisms so little known as these, all such accounts suffer from the serious defect of being based on scanty and, too frequently, inaccurate information. No investigator of these fungi pursues his studies for long before he comes to appreciate the enormous lacunae in our present knowledge of them. It seems useless, therefore, to add another chapter at this time to the already superabundant literature on the subject.

One paper on phylogeny should, however, be read carefully, in the original, by those interested in the lower Phycomycetes—"Endophytische Phycomyceten-Parasiten der Bacillariaceen und einige neue Monaden. Ein Beitrag zur Phylogenie der Oomyceten (Schröter)" by A. Scherffel (1925a). The conclusions of this distinguished Hungarian investigator are of highest importance since they result from first-hand study, over many years, of flagellates, algae, and aquatic Phycomycetes. Very briefly, Scherffel considers that the aquatic Phycomycetes are made up of two distinct series, the "Chytridineen" and the "Saprolegniineen-Peronosporineen." These he believes to have arisen from different monad ancestors, the first from a uniflagellate type, the second from a biflagellate, and to have undergone independent development. Other features are correlated with the flagellation of the zoospore. Within the "Saprolegniineen-Perono-

sporineen" series two subseries are distinguished, the "Saprolegniinae" and "Pythium-Peronosporineae," which have probably arisen from an archetype similar to *Ectrogella*. Although the Monoblepharidales are recognized as distinct in origin and development from both of these series, and probably related to the Blastocladiales, their ancestry is in doubt. For further details and for specific evidence refuting the theories of algal origin of the chytrids and origin from higher fungi the reader is referred to this paper. The present author is thoroughly in accord with the main features of Scherffel's ideas on phylogeny, since they seem best to fit the facts we now know. It can be added, however, that, as a result of discoveries subsequent to the publication of Scherffel's paper, the Monoblepharidales appear to be unquestionably related to the chytrids and might be thought of as a terminal group of the "Chytridineen" series. As Scherffel intimated, the Blastocladiales show undoubted relationships to the chytrids on the one hand, and to the Monoblepharidales on the other.

It is believed that the interpretation of the Chytridiales given here has resulted in the recognition of a compact interrelated group of organisms. The elimination from it of numerous fungi with similar thallus structure but with very different reproductive bodies (for example, the Hyphochytriaceae, the Olpidiopsidaceae, and so on) has not only made the group a more homogeneous natural one but has also reestablished it in its original sense (Sparrow, 1935b). The transference of the simple biflagellate chytrid-like fungi to orders with which they appear to have greater affinities than with the Chytridiales, has, it is hoped, brought about a more natural arrangement of all the lower Phycomycetes. Although the classification would appear to rest primarily on the flagellation of the zoospore, other characters correlated with this are found in the great majority of species, as Scherffel (1925a) has indicated. In the chytrid series the zoospore is posteriorly uniflagellate; its plasma is homogeneous, almost or completely free of granules, and bears a single conspicuous, often large, oil globule. These spores are mono-planetic, and they usually undergo a short rest period or pause immediately after emergence from the sporangium. Their movement, as Cohn (1853) pointed out, is highly erratic, frequently being a hopping punctuated by periods of amoeboid creeping and changes of shape. Other features of the group are noted by Scherffel. Among

these are the gleaming cytoplasm and the resting spores formed by direct transformation—either sexually or asexually—of a cell (the spore usually not resting within a “mother cell” or container). Characteristic of the members of the “Saprolegniineen-Peronosporineen” series are the biflagellate zoospore, the more granular cytoplasm, and a resting spore borne within the lumen of a larger container. The secondary zoospore is somewhat kidney-like or grape-seed-like in shape and bears a shallow longitudinal groove from which two nearly equal, oppositely directed flagella arise. The plasma, in contrast to that of the chytrid zoospore, is granular, no large single globule being formed. The swimming spores in this series show a more or less well defined diplanetism and, save in a very few instances, appear to lack the capacity for amoeboid movement. The movement is an even “automatic” direct one, during which the posterior flagellum trails passively behind. Scherffel considered the vacuolar phenomena occurring in the sporangium during formation of the zoospores in the “Saprolegniineen-Peronosporineen” series to be a further distinction between the two, but recent cytological work (Karling, 1937b; Hillegas, 1940) has not substantiated this difference.

Within the Chytridiales, as here delimited, two series of forms are recognized, the Inoperculatae and the Operculatae, whose members frequently parallel each other in their methods of development and in their thallus structure (Sparrow, 1935b). In the first of these series the zoosporangium opens upon the dissolution of the discharge papilla, forming on the sporangium wall or at the tip of the discharge tube a pore for the liberation of the zoospores. In the Operculatae this pore is formed after the circumscissile dehiscence of a well-defined operculum or cap. The cap is a definite specialized morphological structure and not merely a torn-off portion of the sporangium wall or tip of the discharge tube. Furthermore, the type of discharge is constant in a population of a given fungus and in sporangia subsequently formed by their zoospores. The further interrelationships of the members of the Chytridiales are indicated by the constitution of the families and subfamilies and are chiefly based on methods of development and thallus structure. The Hypochytriaceae are, at present, considered an isolated group of problematical affinities, whose members have, perhaps, evolved from anteriorly rather than posteriorly uniflagellate monads. In spite of their close resemblance in body plan to the chytrids they are

not regarded as being closely allied to them. Each of the orders Blastocladiales, Monoblepharidales, Saprolegniales, Leptomitales, and Peronosporales appears to be composed of clearly related fungi. Whether or not the Lagenidiales as here defined will prove to be a natural group awaits the test of time. Little can be said of the inter-relationships of the members of the Plasmodiophorales until adequate studies have been made of the zoospores and the life cycles of a number of species. This also holds true for their relationship to the Phycomycetes as a whole.

OCCURRENCE AND GEOGRAPHIC DISTRIBUTION

Aquatic Phycomycetes occur on a wide variety of substrata in fresh and, to a lesser degree, in marine waters. Probably the only limiting factors are inimical physical conditions and lack of suitable substrata. Members of the Chytridiales are found as saprophytes or parasites on many diverse hosts, including algae, other aquatic fungi, aquatic and terrestrial herbaceous angiosperms, the spores of pteridophytes and gymnosperms, vegetable debris, the eggs, embryos, and adults of microscopic animals, and the empty integuments of aquatic insects. The Blastocladiales, Saprolegniales, Leptomitales, and Pythiaceae (of the Peronosporales) are predominantly saprophytes, although a few species belonging to the Saprolegniales and Pythiaceae are parasitic on aquatic and terrestrial plants and on aquatic animals. Among the substrata of the fresh-water saprophytes belonging to these orders are twigs, particularly those of ash and birch, rosaceous fruits, and cadavers of fish and insects. The Monoblepharidales are usually found on sunken twigs in cool water, although one member of the order, *Monoblepharella Taylori*, has been isolated from tropical soils on hempseed. The Plasmodiophorales are all obligate parasites of other aquatic fungi and of terrestrial and aquatic (both fresh-water and marine) angiosperms. The Lagenidiales are primarily a parasitic group, usually found on fresh-water algae, fresh-water Phycomycetes, and microscopic animals. The Siroplidiaceae are facultative parasites of certain marine algae.

Although the great majority of the aquatic Phycomycetes occur in fresh waters, the Chytridiales, Saprolegniales, Plasmodiophorales, Lagenidiales, and Peronosporales (one species) all have marine

representatives. Too little is as yet known about marine Phycomyces to make any generalizations as to their occurrence. Most of those Phycomycetes discovered thus far in marine waters are members of the Saprolegniales and the Lagenidiales. These are for the most part chytrid-like forms living in marine algae. A few fungi belonging to one of the uniflagellate groups, the Chytridiales, have been found in the sea, but their occurrence is apparently rare there in comparison with that in fresh water.

From the scanty evidence now available it seems probable that aquatic Phycomycetes are world-wide in their distribution. A comparison of the floras of western Europe and eastern North America, regions in which these fungi have received most attention, reveals no striking evidences of endemism. Scattered accounts from more remote localities, Australia, for example, seem further to confirm their ubiquity.

COLLECTION

The supposed rarity of many of the aquatic Phycomycetes appears to be due largely to a lack of knowledge of proper methods of collection. It must be admitted, however, that some are, in fact, of very infrequent occurrence.

The aquatic Chytridiales utilize a variety of substrata, namely, algae, other aquatic Phycomycetes, decaying plant debris, microscopic animals and their eggs, and exuviae or empty integuments of aquatic insects.

Several methods are used in obtaining inhabitants of fresh-water algae. The first of these is by the microscopic examination of large amounts of material immediately after collection. This is a laborious process, but it is necessary for those forms which are unusually sensitive to environmental conditions and which are unable to withstand change. Another method is to place the material (small mats of filamentous algae, scum of *Euglena*, and the like) immediately after collection in shallow dishes of water in diffuse light, care being taken to avoid overcrowding. Frequently, these conditions favor the development of fungi, and in a few days a variety of chytrids often appear. Still another and, perhaps, the most successful method is to set up a gross culture of a fairly hardy alga, such as *Cladophora*, and place in it bits of boiled algae, pollen, and herbaceous

stems. After a few days such "baits" frequently yield interesting fungi. The algae on which chytrids are most often found are members of the Zygnematales (Conjugatae), Oedogoniales, and Ulothrichales (particularly *Cladophora*). Usually both living and dead plants of *Nitella* and *Chara* harbor an interesting chytrid flora. Chytridiaceous fungi are frequently found on filamentous water molds, such as *Achlya* and *Saprolegnia*, in old gross water cultures. Bits of plant debris from aquatic sites occasionally yield chytrids upon direct microscopic investigation. A surer method, however, is to prepare gross water cultures with such debris, into which are put as bait small pieces of soft stem tissues, such as corn or grass culms, or bits of leaves of *Anacharis* or *Acorus*, or root tips. Care should always be taken to maintain a proper balance between the amount of organic debris and the volume of water, so as to prevent fouling of the culture. Most gross cultures of algae and debris support a population of microscopic animals, usually rotifers and nematodes. The adults and their eggs should be watched for evidences of parasitic organisms, and all dead animals should be examined carefully for traces of fungi. The layer of scum formed on the sides of the culture jar at the water line is a particularly favorable place to find them. One of the most curious and productive habitats for chytrids is the empty cases (integuments or exuviae) of aquatic insects such as caddis flies, May flies, midges,¹ and the like. After the insect emerges from the water and sheds its skin this integument is frequently washed back into the water. Within it no doubt persist the remnants of the molting fluid, which are attractive to the zoospores of certain chytrids. These fungi soon establish themselves within the integument and may flourish there in great abundance for a few days, after which they either disappear or form resting spores and become quiescent. It is possible that the material of the integument itself is utilized by the chytrids, but this does not seem probable in view of the rarity of their occurrence in integuments which have obviously been in the water for a long period. The collection of the exuviae offers no difficulty if they are searched for in early spring among stands of emergent phanerogams such as *Scirpus* or *Juncus* in shallow water.

Members of the Blastocladiales occur for the most part in two

¹ Although dragonfly exuviae are excellent habitats for chytrids, they are too large and opaque for good observation of the fungi.

very different habitats. The most ubiquitous genus of this order, *Blastocladia*, is primarily an inhabitant of submerged twigs and rosaceous fruits. On these two substrata it forms white, generally rather crisp and granulated hemispherical pustules of densely compacted plants. The collection of fruit- and twig-inhabiting fungi is a relatively simple matter. Such substrata can be searched for at a likely aquatic site, but a surer method is to place twigs of ash or birch, or apples, pears, or the like in a galvanized perforated metal container or closed test-tube basket, or one of wire screening, and submerge it—well concealed and anchored—in a favorable locality. After a month or more the material can be brought back to the laboratory in a jar or in very wet paper, the surrounding slime (which should be examined for pythiaceous fungi) washed off, and samples made of various pustules and filamentous fungi. This material should be worked intensively immediately after collection, since the changing environmental conditions generally induce quick zoospore production. Samples of minute pustules as well as of the larger ones should be made, for the former are not always merely immature plants of larger species but often belong to totally different ones. Submerged fruits and twigs are a prolific source of other fungi as well as of *Blastocladia*. For example, *Macrochytrium*, a chytrid, *Gonapodya* and *Monoblepharis*, members of the Monoblepharidales, and *Apodachlya*, *Rhipidium*, *Sapromyces*, *Araiopora*, and *Mindenella* of the Leptomitales have all been reported from these substrata.

The other habitat in which members of the Blastocladiales occur is soil. Although species of *Allomyces*, the commonest terricolous form, are occasionally found in standing water, they have been isolated most often from either permanently or periodically wet soil. In the preparation of water cultures with soil samples battery jars full of water are sterilized. After the water has cooled, the soil (about one or two tablespoonfuls are sufficient) is dumped in and the culture baited with appropriate substrata. Boiled split hempseed or cadavers of fruit flies are the bait most frequently used. In the isolation of *Allomyces* it appears almost essential that a large volume of water cover the sunken bait.

Like the closely related Blastocladiales, the members of the Monoblepharidales have been collected from standing water and from soil. Species of *Gonapodya*, as has previously been mentioned, may be found on submerged twigs and fruits. *Monoblepharis*

occurs for the most part on old undecorticated sunken twigs, particularly of birch and ash, in clear, often cool, water. If a few such twigs are placed in battery jars of pure water and left at about 11° C., the growth of *Monoblepharis* is particularly favored. The fungus may form dense pustules or a complex of delicate hyphae covering the whole twig. *Monoblepharella* has, thus far, been recovered only from tropical soils, where it often occurs with *Allomyces* (see above). It grows readily on hempseed bait.

Those members of the Plasmidiophorales which are parasitic on aquatic Phycomycetes are sometimes found in old gross water cultures. The fungi parasitic on aquatic phanerogams produce (with the exception of *Ligniera*) conspicuous hypertrophy of the host, a fact which aids in the recognition and collection of infected material.

The simpler members of the Saprolegniales (Ectrogellaceae, Thraustochytriaceae) occur on fresh-water and marine algae. Species of *Ectrogella* often develop in Petri dishes of fresh-water diatomaceous scum left in a cool light place in the laboratory for a few days. One marine form, *E. perforans*, is very common on marine species of *Licmophora*, a stalked diatom epiphytic on littoral seaweeds. Parasitic marine forms such as *Eurychasma* and *Eurychasmidium* are local; the former, for example, has been found by the writer to occur in the Kattegat only on the phaeophycean *Striaria* growing on a clay bottom. The rhodophycean *Ceramium* infected by *Eurychasmidium* may frequently be detected by the presence on it of numerous short, abnormal, lateral branches. *Thraustochytrium*, a monotypic marine genus, has thus far been collected only on disintegrating plants of the green alga *Bryopsis* and on the rhodophycean *Ceramium diaphanum*. It is usually found on material in shallow dishes into which fresh sea water is allowed to drip constantly. Saprophytic species of the Saprolegniaceae occur on bits of substrata of both plant and animal origin. The cadavers of insects or their larvae, dead fish, twigs, flowers, fruits, and so on, are all favorable sources of food. In recent years the split boiled seed of hemp (*Cannabis sativa*) has been introduced as a substratum by investigators at the University of North Carolina. Extensively used as bait as well as for the maintenance of these fungi in gross water cultures, it has proved an exceedingly favorable medium, with the distinct advantage of being less likely to become fouled by bacteria and protozoa.

than are flies, grubs, and the like. A number of interesting fungi belonging to the Saprolegniaceae have been isolated from the soil (Harvey, 1925, *et al.*) by methods similar to those described by Butler (1907) for the collection of species of *Pythium*. In contrast to the technique noted above for the isolation of *Allomyces*, here only a thin layer of water covers the soil and the bait is allowed to float on the surface of the water as well as to rest in direct contact with the earth. Since a few of these fungi lack a motile stage, actual contact of some of the bait with the soil is essential.

The Leptomitales occur primarily as inhabitants of fruits and twigs. The methods of collection outlined for members of the Blastocladiales in a similar habitat apply here as well. *Leptomitus* has been most frequently found in water polluted by decaying organic material, such as that in the outlets of drains, sugar-beet factories, and the like.

Olpidiopsis, the commonest member of the Lagenidiales often appears in gross water cultures of saprolegniaceous Phycomycetes. The three predominantly marine genera, *Petersenia*, *Sirolpidium*, and *Pontisma* often develop in algae which have been in a tank of running sea water for from several days to a week. *Sirolpidium* occurring in *Bryopsis* frequently causes blackened areas on the frond which are recognizable to the naked eye. Its greatest development, however, takes place after it has remained under laboratory conditions for a few days. Species of *Myzocytium* and *Lagenidium* are infrequently collected. Algal mats, particularly those composed of Conjugatae, must be systematically examined microscopically for the presence of these fungi.

The species of the Pythiaceae considered here are, for the most part, saprophytes of fruits and twigs, occurring with such forms as *Rhipidium*, *Gonapodya*, and so on. *Zoophagus*, however, has usually been found ramifying between filaments of green algae, or among plants of the Characeae.

ISOLATION AND CULTURE

Many of the species of fungi discussed in the present work can be isolated by ordinary methods and cultivated on a variety of prepared solidified media. Particularly is this true of members of the Pythiaceae, Saprolegniaceae, and Blastocladiales. By far the greater num-

ber of species, however, have neither been isolated in unifungal culture nor been induced to grow on artificial media. Since the evidence now being slowly accumulated shows very definitely that many of these are capable of growth under the artificial conditions of laboratory culture, it is evident that a wide field for the investigation of their nutritional requirements exists.

The development of methods for the isolation and cultivation of chytrids¹ has received increasing attention in very recent years, and great progress has already been made. Zopf (1887) long ago pointed out that some chytrids could be isolated from water on fern spores or pollen grains. The bait could be dropped into a large sample of pond water (one liter or more) and watched for fungi. By transferring to sterile water, with a sterile needle, a pollen grain having a single ripe sporangium and adding new pollen grains a unifungal culture could be established. Since this sporangium was formed from a single zoospore, the culture started from it, if no other plants were present on the pollen grain, was the equivalent of a single-spore culture. This method has been used with success by Couch (1939a) and his students in developing unifungal cultures of a number of chytrids. Couch has found pollen of *Liquidambar* a particularly favorable substratum for this work. Unifungal cultures have been reported by other investigators. Minden (1902) briefly records the isolation and cultivation on plum (or prune) gelatin of an unnamed member of the Rhizidiaceae, but he does not indicate whether or not the cultures were free from bacteria. Sparrow (1931c) isolated filaments of *Spirogyra* infected with *Cladochytrium replicatum* and, after washing them thoroughly in sterile water, planted them in dishes of maize agar. The fungus spread out from the algal thread into the medium. Because of the chytrid's slow rate of growth, however, it could not be freed of bacteria. J. Bayley Butler and Humphries (1932) secured outgrowths of *Catenaria Anguillulae* from infected liver-fluke eggs and growth from zoospores when these were placed in fluke-ova extract and flaked coagulated egg albumen. Growth also occurred in this extract when agar (0.25 per cent) had been added to it. Other chytrids have been secured in unifungal culture by various investigators, notably Karling (1937a), Berdan (1939), Haskins (1939), Ward (1939), and others.

Couch (1939a) cites several methods which have been found par-

¹ See Whiffen, *J. Elisha Mitchell Sci. Soc.*, 57: 321. 1941.

ticularly effective in securing unifungal (but not bacteria-free) cultures from materials such as decaying grass leaves infested with various chytrids. He describes these in (1)-(4) below:

(1) Isolation in water of a single sporangium or (2) isolation on agar of a single sporangium; (3) isolation of spores from a single sporangium on slide; (4) isolation of single spore in a capillary tube or (5) isolation of single spore on agar or (6) isolation of a single thread or several threads on agar.

With method (1) the procedure may be as follows: Place leaf with chytrids in a drop of water in a Petri dish and in another drop of water about one cm. away in the same dish put a new piece of sterile leaf. Then under a wide field binocular dissecting microscope ($\times 40 - \times 100$) with sharp, smooth, steel needles dissect out a small piece of leaf to which only one sporangium is attached. Transfer this to a small drop of water in the same dish and examine under compound microscope to be sure only one sporangium and no spores are present. The fragment of leaf with the sporangium may now be transferred to the fresh piece of leaf. All transfers up to this stage are made from drop to drop in the same dish, because if the delicate chytrid were transferred from one dish to another, it might dry up in the operation. After the chytrid sporangium is on the large, moist leaf, the latter is transferred to a drop of charcoal water in a fresh sterile dish and other drops of water are added to the floor and ceiling of the dish to prevent desiccation. In this operation many of the single sporangia are injured in transfer. Hence it is advisable to make large numbers of transfers.

If one is lucky, each isolated sporangium will form zoospores which will infect the new leaf, thus establishing the chytrid in pure culture save for the presence of bacteria.

The above technic is useful only if the sporangia are large. A more useful technic (2), particularly with small sporangia, and where several species are mixed and are discharging spores simultaneously, is as follows. An infected leaf is transferred after washing to the surface of a 3% agar plate The desired chytrid sporangium is now dissected out from the leaf tissue and dragged along on the surface of the agar to free it from spores, bacteria, etc. After examining under the compound microscope to make sure that only one chytrid sporangium is now present, it is cut out with a little cube of agar and transferred to a fresh Petri dish in a drop of water with a fresh piece of leaf, other drops of water being added to the bottom of the dish to prevent desiccation. This is a very useful technic because it enables one to transfer nothing but the sporangium and its rhizoids. We have used a slight modification of this method by tearing the leaf tissue apart on the surface of the agar and spreading it out. If water is present, some of the sporangia may discharge their spores on the surface of the agar. The spores may then germinate in contact with the leaf, sending their rhizoids into the

agar. It is possible then to remove the leaf, wash the surface of the agar with water from the wash bottle and then to dissect out one sporangium from the agar surface.

If the rhizoidal system is very complex and the spores of other fungi abundant, the method just described may be unsatisfactory, in which case the following method (3) is useful. A single sporangium about ready to discharge spores is isolated by method 1 or 2 and put on a sterile slide in a drop of water and kept under observation so that one may determine just when the spores emerge. The moment this happens some of the spores are drawn up in a capillary tube and blown out in a drop of water with a piece of sterile leaf in a fresh Petri dish. If ordinary care is used one may secure cultures by this technic descended from a few spores. It is possible so to perfect this method that one can, with a little practice and skill, make single spore cultures. This may be done as follows: (4) By using a very fine capillary tube and picking up only a few spores, then diluting the spores by mixing in another drop of water and so on by further dilutions, it is possible finally to get only one or two spores in the capillary tube. If the tube were clean to begin with, it may be examined on the surface of the Petri dish to determine how many spores it contains. If only one spore is present, the tube is then transferred to a drop of water containing a piece of leaf. If it contains two or even several spores, it is possible to break the tube in such a way that one can separate a single spore from the others.

The securing of bacteria-free cultures of chytrids on artificial media has been difficult, owing primarily to the slow rate of growth of the rhizoidal system and, in many species, to the monocentric nature of the thallus. Couch's methods 5 and 6 refer to the preparation of bacteria-free cultures:

So far we have developed two methods for doing this. The easier, if the spores will germinate on agar, is by the isolation of a single spore on agar (5). After much experimenting with spore germination on nutrient agars, we have found several which are useful in this work.

1. Plain agar 3% (the agar shreds should be washed over night in several changes of water to free from trash).
2. Agar No. 12 (Leitner's agar) 2% agar and 0.004% peptone (meat).
3. Agar No. 13 (Foust's agar) 2% agar and 0.15% maltose and 0.004% peptone (meat).
4. Corn meal agar (use 2-4 heaping teaspoons full to 1 litre water, depending upon strength desired. Heat gently in water bath, temperature about 60°, 1 hour. Filter. Add water to make 1 litre. Agar 2%).

The spores seem to germinate better on plain agar or agar with very small amounts of nutrient material. Before taking time to spread the spores carefully on agar it is worth while to drop a few on the medium used to determine whether or not the spores go to pieces or settle down and encyst. Naturally if the spores are plasmolized by the nutrient agar it is a waste of time to go further with that particular medium. Spores to be isolated should be as free from bacteria as possible. Hence, it is well to isolate one or a few sporangia about to discharge spores in a drop of water on a sterile slide. However, where only a few spores are available it is possible to pick them up with a platinum loop or a small pipette directly from the original dish. The essential part of this technic is to spread the spores so well on the surface of the agar that some of the spores will be completely separated from the bacteria and other organisms. A successful spreading requires a firm agar (2-3% agar) and a steady hand. The spores are picked up with a platinum loop and the loop dragged along the surface of the plate in a straight line. Several east-west lines may be made and then another group of north-south ones. It is unnecessary to mark these lines for the bacterial colonies will make the lines quite evident. If the laboratory is clean and free from spores of *Penicillium*, etc., it is possible to do this spreading with the uncovered dish on the table. However, if the air is dusty, the dish should be held at an angle with the agar surface down. If the spores germinate at all they will germinate within 12 to 24 hours or in even less time. After 12 hours the plate should be examined under the binocular dissecting microscope ($\times 40 - \times 100$). If the spores have been properly spread, one may now cut out a tiny block of agar with a single sporangium descended from a single spore. The cutting out operation requires a very fine tool. For this we use a tiny chisel made by sharpening down a steel needle under the microscope. Individual sporangia may be transferred to a drop of water in a sterile Petri dish on a piece of leaf. Such a culture descended from a single spore may be kept free from bacteria for a few generations in water cultures. In some chytrids the sporangia mature and discharge their spores on agar. It is possible, though exceedingly tedious, to keep such cultures pure, growing on agar and free from bacteria. The labor involved, however, is excessive and we have carried such cultures on agar for only a few generations.

In some of the polycentric chytrids as *Cladochytrium replicatum* the spores germinated on agar to produce a distinct mycelium. It is therefore possible to isolate this species by cutting out a single thread or several threads. This method (6), however, is useless with the monocentric chytrids.

Recently opportunity was afforded the author to examine a pure, bacteria-free culture of a chytrid, possibly *Rhizophlyctis rosea*, iso-

lated and grown by R. Y. Stanier. He has outlined the methods (personal communication) used in its isolation and culture as follows:

The present isolation of *Rhizophlyctis rosea* was greatly facilitated by the fact that it first appeared in a highly selective enrichment culture. The enrichment medium—prepared in an attempt to isolate cellulose-decomposing myxobacteria—consisted of a mineral agar plate covered with a round of filter paper, which was inoculated with compost and incubated at 28° C. After four days the filter paper had become entirely covered with a bright pink growth. Microscopic examination showed the presence of large numbers of typically chytridiaceous thalli. The culture was maintained in crude form for several weeks by repeated streaking of pieces of attacked filter paper on fresh plates, but such treatment did little to reduce the large number of contaminating organisms originally present, and it became clear that other methods of purification would have to be adopted.

When a piece of filter paper heavily invested with mature thalli was placed in water, spore discharge occurred almost simultaneously from numerous zoosporangia after a period of from 20 minutes to half an hour. This phenomenon suggested a convenient method of purification. Large pieces of attacked filter paper were removed from a gross culture and put in the bottoms of test tubes containing 10–15 cc. of sterile tap water, where they were left undisturbed until after spore discharge had begun. Since the zoospores move more rapidly than bacteria and are in addition strongly aerotactic, they soon accumulated in large numbers in the upper layers, accompanied by only a few bacteria. At this stage, microscopically controlled, loopsful of the surface water were removed (care being taken to avoid agitation of the tube) and streaked on mineral dextrose agar plates, which were incubated at 28° C. After 24 hours the plates were examined under a dissecting microscope; numerous small thalli were seen interspersed among the bacterial colonies. The positions of uncontaminated thalli well separated from bacterial colonies were marked on the bottoms of the plates with India ink, and the cultures reincubated until spore discharge had taken place (this took on the average an additional 12–36 hours at 28° C.). At the time of discharge a small amount of liquid was exuded from the zoosporangia but rapidly reabsorbed by the agar, after which the spores lay motionless in small fields surrounding the empty spore cases Under the dissecting microscope a mass of such spores was picked up on a sterile needle, transferred to a drop of sterile water on another mineral dextrose agar plate, mixed with the water and streaked. With proper precautions, the air contamination incidental to manipulating an open plate under the microscope is negligible; thus the second plates yielded either pure cultures or else cultures whose

further purification presented no difficulties. One point concerning the isolation technique deserves special mention. For both the first and second streakings it is highly desirable, if not essential, to use *well-dried* agar plates, so that after inoculation no water remains on their surfaces. If this is not done, isolation of the chytrid may be impossible due to the rapid spreading of motile bacteria always present in the enrichment cultures. I have found that the most convenient way of getting dry plates is to pour them 3-4 days before use.

In order to make perfectly sure of the purity of cultures, zoospores from the first plate showing no bacterial colonies were streaked once more as previously described, and only from these latter plates was material taken for pure culture slants. In addition, the purity of stock cultures was checked at frequent intervals by microscopic examination.

Probably all members of the Blastocladiales are culturable on ordinary artificial media. *Blastocladia* appears to be the most recalcitrant, seemingly only one instance being recorded (Emerson, in Blackwell, 1940) of its successful cultivation on agar.

With the exception of *Monoblepharella Taylori*, which has been cultivated on a variety of common liquid and solid media, no members of the Monoblepharidales appear to have been grown in pure culture on artificial substrata.

Although the higher members of the Saprolegniales have nearly all been brought into culture, the minuteness and the simple nature of the thalli of members of the Ectrogellaceae and the Thraustochytriaceae make them exceedingly difficult forms to propagate.

Of the Leptomitales, *Leptomitus*, *Apodachlyta* (see Schade, 1940), and *Sapromyces* (Bishop, 1940) have been cultured. Minden (1916) records the growth of *Rhipidium interruptum* in dextrose and peptone solutions, malt gelatin, and the like. *Araiopora spinosa* was cultured by him on plum-decoction gelatin and in malt and bouillon broth. Despite repeated attempts by subsequent investigators no species of *Rhipidium* and *Araiopora* have since been successfully grown on artificial media (see Kanouse, 1927). For the most part, the members of the Lagenidiales have not been brought into pure culture. *Lagenidium giganteum*, however, has been grown in bacteria-free cultures on various laboratory media (Couch, 1935b). A slight growth of the marine fungus *Siroloidium Bryopsidis* has been secured in weak dextrose solutions (Sparrow, 1936b).

PRESERVATION

The most useful method in preserving aquatic Phycomycetes so as to make them readily available for examination is by the preparation of permanent mounts. Water mounts of material are mordanted with a weak solution of acetic acid; they are then washed and eosin in 10 per cent glycerin solution is run under the cover glass. After the solution has concentrated to pure glycerin and eosin, the slide is sealed with a cement. When tightly sealed such preparations last for many years. In dealing with minute forms such as chytrids on algae, in which the material may frequently be very scanty, either the infected substrata may be isolated on another slide and preserved or the whole lot of material may be preserved on the slide and the region where the infected filament lies encircled with India ink.

Dr. A. F. Bartsch, of the University of Wisconsin, has kindly outlined, in a personal communication, a method he has used with excellent results on material of *Blyttiomycetes spinulosus*, a parasite of the zygospores of *Spirogyra*. His procedure may be summarized as follows: The material is fixed in a small vial in formalin-acetic acid alcohol (glacial acetic acid, 5 c.c.; commercial formalin, 5 c.c.; 50 per cent ethyl alcohol, 90 c.c.) for three days. It is then washed by adding small amounts of water to the vial, shaking slightly, and pouring off the fluid. This is continued until the odor of the acetic acid is gone. The water is now poured off again and a solution of 0.5 per cent iron alum is added. After twelve hours the iron alum is washed out with three changes of water. About seven drops of 1 per cent haematoxylon in 95 per cent alcohol is then added to 10 c.c. of water and poured over the material, which is allowed to stain for three days, after which it is washed in tap water (alkaline) several times. Next it is destained in 2 per cent iron alum, a sample being watched under the microscope until the destaining is satisfactory, when the iron-alum solution is poured off and the material is washed in six changes of water and placed in 10 per cent glycerin in an open Petri dish. After the glycerin has become concentrated the alga is mounted in glycerin jelly on a slide, a round cover glass is added, and the whole is sealed with balsam.

Another method found useful by Bartsch for fungi infecting plankton algae (but not filamentous forms) is to mount directly in

Zirkle's fluid¹ and after a half hour to ring the preparation with balsam.

Large amounts of material, previously fixed and killed, may be preserved in 70 per cent alcohol to which a small amount of glycerin has been added. Dr. H. E. Petersen, of the University of Copenhagen, has pointed out that formalin solutions are not good preservatives for chytrids, since the rhizoids of the fungi do not keep well.

The precise methods necessary for the preparation of material for cytological studies may be found in the papers dealing with this aspect of the aquatic Phycomycetes (see discussions of the cytology of the different orders in the text).

KEY TO THE ORDERS OF THE AQUATIC PHYCOMYCETES

Zoospores posteriorly uniflagellate, formed inside the sporangium

Thallus either lacking a vegetative system and converted as a whole into reproductive structures (holocarpic) or with a specialized rhizoidal vegetative system (eucarpic) and one (monocentric) or more (polycentric) reproductive structures; zoospore usually bearing a single conspicuous oil globule

CHYTRIDIALES, p. 21

Thallus nearly always differentiated into a well-developed vegetative system, often hypha-like, on which are borne numerous reproductive organs; zoospore without a conspicuous globule

Thallus usually having a well-defined basal cell anchored in the substratum by a system of tapering rhizoids; resting structure an asexually formed thick-walled often punctate resting spore; sexual reproduction by means of isogamous or anisogamous planogametes; alternation of generations present in some species ... BLASTOCLADIALES, p. 391

¹ Zirkle's fluid may be prepared as follows:

Glacial acetic acid	45 c.c.
Water	55 c.c.
Glycerin	5 or 10 c.c.
Gelatin (powdered)	10 gms.
FeCl ₃	0.02 gm.
Carmine	to saturation

Stir the gelatin with water until it forms a paste. Then add glycerin, acetic acid, iron salt, and carmine in order. Boil one minute and filter.

AQUATIC PHYCOMYCETES

Thallus without a well-defined basal cell; composed of delicate much-branched hyphae; resting structure an oöspore; sexual reproduction oögamous, the male gamete always free-swimming, the female devoid of a flagellum

MONOBLEPHARIDALES, p. 443

Zoospores anteriorly uniflagellate, usually formed outside the sporangium..... HYPHOCHYTRIACEAE,¹ p. 477

Zoospores (at least the secondary ones) with two oppositely directed flagella, formed either inside or outside the sporangium

Zoospores with a very short anterior flagellum and a long posterior one; thallus wholly endobiotic, holocarpic, forming a zoosporangium or a sorus of zoosporangia or resting spores

PLASMODIOPHORALES, p. 487

Zoospores with two flagella of approximately equal length, which are oppositely directed in the secondary zoospores; thallus endobiotic and holocarpic or eucarpic and both intra- and extramatrical; sexual reproduction oögamous

Zoospores always cleaved out within the sporangium, diplanetic, the primary zoospore motile or encysting immediately after discharge, or completely suppressed (i.e. only secondary zoospores formed)

Thallus holocarpic or eucarpic; the hyphae in eucarpic forms without constrictions or cellulin plugs, not arising from a well-defined basal cell; oögonium with one or more eggs

SAPROLEGNIALES, p. 511

Thallus eucarpic; the hyphae bearing constrictions accompanied by cellulin plugs, usually arising from a more or less well defined basal cell anchored in the substratum; oögonium (with the exception of *Apodachlyella*) with a single egg

LEPTOMITALES, p. 543

Zoospores cleaved out either within the sporangium or partly or wholly formed outside the sporangium, where they are usually surrounded by a more or less evanescent vesicle; motile spore always² of the secondary type

Primarily aquatic; the thallus holocarpic, endobiotic, either unicellular or consisting at maturity of a series of unbranched or rarely branched segments of slight extent; zoosporangia persistent

LAGENIDIALES, p. 591

Primarily terrestrial; thallus eucarpic, mycelial, and usually both intra- and extramatrical; zoosporangia persistent or deciduous (conidia)

PERONOSPORALES, p. 679

¹ See remarks on p. 477.

² Scherffel (1925a) has reported primary flagellated zoospores in *Olpidiopsis Oedogoniarum*.

UNIFLAGELLATAE

CHYTRIDIALES

THE discovery of the fungous nature of the aquatic chytrids and their recognition as a taxonomic entity are due for the most part to the researches of Alexander Braun. It is clear that as early as 1846 Braun (1856a:22) had observed chytrids on the fresh-water algae *Hydrodictyon* and *Stigeoclonium* and was aware of their parasitic rôle. In his *Betrachtungen über die Erscheinung der Verjüngung in der Natur* (1851), he formally established the genus *Chytridium* with one species, *C. olla*, which was parasitic on the oögonia of *Oedogonium*. To be sure, there were descriptions in the literature prior to Braun's paper of organisms now known to be true chytrids (species of *Synchytrium*, *Physoderma*, and *Micromyces*), but their affinities and, indeed, in some instances, their parasitic nature were not understood. Gross (1851), in connection with a curious account of supposed polymorphism and metamorphism in lower plants and animals, described and figured a chytrid identifiable with *Polyphagus Euglena*. Thwaites (1846-47), Shadbolt (1852), and other algologists gave the term "asterospheres" to spiny spheres found by them in vegetative cells of Conjugatae. As late as 1860 Pringsheim interpreted the zoospores of an endobiotic chytrid (now known as *Pringsheimiella*) parasitic on a sterile *Achlya* as the antherozoids of the host, and other examples might be cited. With the publication of Braun's classic series of papers on *Chytridium* (1855a, 1855b, 1856a, 1856b), the small group became well established and their true nature generally recognized.

Included in Braun's *Chytridium* was one supposed chytrid, *C. Saprolegniae*, whose zoospores were not observed and which probably was not related to his other species. It came to be identified with fungi which were observed by Nägeli (1846), Cienkowski (1855), and Cohn (1853, as *Peronium aciculare*) and which were all probably species of *Olpidiopsis*. Subsequently a number of other one-celled aquatic fungi resembling superficially Braun's species of *Chytridium*, but differing, as did *C. Saprolegniae* (Cornu, 1872a), in the num-

ber of flagella on the zoospore, were gradually added to the group. As a result, the "chytrids" soon became a dumping ground for all aquatic Phycomycetes of simple body plan.

In 1865 De Bary and Woronin recognized the chytrids as a family made up of the genera *Chytridium*, *Rhizidium*, and *Synchytrium*. Cohn (1879:279) made the group coequal with the Saprolegniales and Peronosporales, and it has usually been so regarded by most students of the Phycomycetes. In the well-known monograph by Fischer (1892), however, the chytrids are combined with the Acanthostyles (Lagenidiales) to form the Archimycetes, coequal with the Zygomycetes and Oomycetes. This merging of the two groups has been followed by few subsequent workers, although the term "Archimycetes" has been retained by some and applied to various combinations of lower fungi.

The minute and often bizarre fungi belonging to the Chytridiales are found predominantly in fresh waters, although a few occur in the ocean and in terrestrial or semiterrestrial habitats. In fresh water they most often appear on algae, other aquatic Phycomycetes, spores and decaying parts of higher plants, on microscopic animals and their eggs, and in the empty exuviae of certain aquatic insects. Of the few marine species now known nearly all have been discovered on seaweeds; one as yet little-understood marine form has been recorded from the ductless kidney of ascidians. Relatively few are obligate parasites of phanerogams. Chytridiaceous fungi have been found wherever they have been searched for by trained observers and are probably world-wide in their distribution. At present the best-known areas are western Europe and eastern North America, where most of the investigations on these fungi have been undertaken.

The most striking characteristics of the chytrids appear to be their simple body plan, their vegetative system of strongly tapering rhizoids, and their posteriorly uniflagellate zoospores, which often exhibit a hopping motion and which contain a highly refractive oil globule. The purely vegetative part of the thallus, if formed, is ordinarily inconspicuous because of its tenuity, but nonetheless it may be exceedingly widespread and profusely branched. Only one reproductive structure is produced on the thallus in the majority of these fungi; its rudiment is for the most part clearly differentiated from the less obvious vegetative system, and when reproductive activity is culminated the whole plant body usually disintegrates.

In a few chytrids, however, more than one center of thallus organization is formed, some or all of which may ultimately be converted into reproductive organs.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

Establishment and Development

Considerable differences exist among the chytrids with respect to their relation to the substratum. In some the thallus may be formed completely within the substratum (endobiotic). In others it is partly on the outer surface (epibiotic) and partly within, the two components being separated by the wall of the substratum. In this situation the outer part (which frequently becomes the reproductive organ) and the inner (the nutrient-gathering system) are joined by a narrow tube formed from the penetration tube of the infecting zoospore. In a third type of relationship the reproductive rudiment and the bulk of the rhizoidal system radiating from it lie free in the water among the sources of nutrition, only the tips of the rhizoids penetrating the nutrient material (interbiotic).

It is difficult to make any generalizations in regard to the establishment and development of the thallus in the Chytridiales, since its members often differ so widely in these respects. Taken as a whole, however, certain principal types may for practical purposes be recognized, to each of which may appropriately be applied the genus name of the fungus which most nearly exemplifies it, that is, (1) *Olpidium* type, (2) *Entophyscias* type, (3) *Chytridium* type, and (4) *Rhizidium* type. Other well-marked types may also be discerned, but they either are regarded as variations or elaborations of those already named or are so unique and occur in so few forms as to merit individual attention. This arbitrary grouping is to be considered in no other light than that of convenience. In the present state of our knowledge of the chytrids it is impossible to make any sweeping statements concerning the derivations and interrelationships of developmental types. It is apparent, however, in taking the lower aquatic Phycomycetes as a whole, that certain of these types occur not only in both the operculate and the inoperculate chytrids but in other orders as well. Thus the *Olpidium* type is found in the Chytridiales (*Olpidium*, *Endochytrium oophilum*), the Hypochytriaceae (*Latrostium*), the Saprolegniales (*Ectrolegella*), and

the Lagenidiales (*Olpidiopsis*, *Sirolpodium*, *Lagenidium oophilum*, and so on). The failure to recognize the fact that parallel body types have arisen independently in these different groups has greatly confused and retarded significant studies on the taxonomy and phylogeny of the lower aquatic Phycomycetes (Sparrow, 1933a, 1935b).

In the first three of the developmental types about to be described actual entry of the fungous protoplasm into the substratum (a process probably first observed by Kloss, 1856a) is accomplished by means of a tenuous tube produced by the encysted zoospore. This tube, probably aided by enzyme action, penetrates the wall of the substratum and either conveys a part of the contents of the spore into the interior or retains the contents, its tip then elongating and laying down the rudiments of the vegetative system. In the fourth or *Rhizidium* type only the distal parts of the rhizoids emanating from the encysted spore make contact with and enter the substratum.

1. *Olpidium* type.—After the tip of the penetration tube in the *Olpidium* type has reached the lumen of the host cell the contents of the encysted zoospore are conveyed to the inside (Fig. 1 A, p. 26). Here the naked mass is surrounded by a pellicle, which soon becomes a discrete wall. With growth the young thallus may assume a spherical or ellipsoidal shape and in parasitic forms be carried away, perhaps by cytoplasmic movements of the host, from the open tip of the penetration tube. This tube, as well as its attendant epibiotic cyst, usually disintegrates and takes no further part in the developmental cycle. Inside, the young thallus absorbs materials over its whole surface and increases steadily in size. No specialized vegetative parts are formed, and at maturity the body, which is completely within the substratum (endobiotic), becomes converted as a whole into a reproductive structure (holocarpic). The zoospores in the sporangia of endobiotic types are conveyed to the outside by a more or less well developed discharge tube, the tip of which is extramatrical. Such a type of development is characteristic of the Olpidiaceae. It is elaborated in the Achlyogetonaceae, in which family the thallus is cylindrical, and at maturity becomes segmented into a linear series of sporangia. Another variation is found in the Synchytriaceae, in which sorus formation takes place.

2. *Entophyscites* type.—In the *Entophyscites* type (Fig. 1 B, p. 26), the endobiotic tip of the penetration tube remains filamentous, elong-

gates as it drains the cyst of its contents, and lays down within the substratum the main axes of the branching rhizoidal system. The elements of the vegetative system just beneath the substratum wall then expand to form the rudiment of the reproductive structure. In the majority of the fungi exhibiting this sequence of development the empty cyst and the penetration tube disintegrate and play no further part. Thus the incipient reproductive structure arises secondarily¹ by expansion of those elements of the vegetative system immediately beneath the wall of the substratum, often including portions of the primary branches. Both vegetative and reproductive parts are, therefore, developed endobiotically. The zoospores reach the outside medium by the formation of a discharge tube, as in the previous type.

Since here, as is not true of the *Olpidium* type, structures of a purely vegetative nature (the rhizoids) are formed, as well as a reproductive rudiment, this and succeeding types of thalli are said to be "eucarpic," that is, they are differentiated into sterile and fertile portions. If, as in the majority of eucarpic types, only a single reproductive rudiment is developed on the thallus, the thallus is said to be "monocentric," whereas if more than one is formed (as in *Cladochytrium*), it is termed "polycentric" (Karling, 1932). The rhizoids of all eucarpic thalli are probably conveying materials back to the enlarging reproductive rudiment at all times during their elongation into the substratum, except when they are first being established. When extension of the rhizoids ceases the residue of materials within them is soon drained into the future reproductive body, which is then delimited by a septum from the now empty vegetative system.

Variations and elaborations of the *Entophyscias* type may be found among both operculate and inoperculate chytrids. Indeed, the *Chytridium* type itself may be regarded as one of these variations. Since it occurs with great frequency, however, it is kept separate here. No attempt is made to decide whether the endobiotic or the epibiotic center of thallus organization is the more primitive, or whether one has been derived from the other.

3. Chytridium type.—The early stages of the *Chytridium* type (Fig. 1 C, p. 26) resemble those of the *Entophyscias* type. After

¹ Observations on the development of *Endochytrium operculatum* by Hillegas (1940:9) indicate that the rudiment may sometimes be formed first.

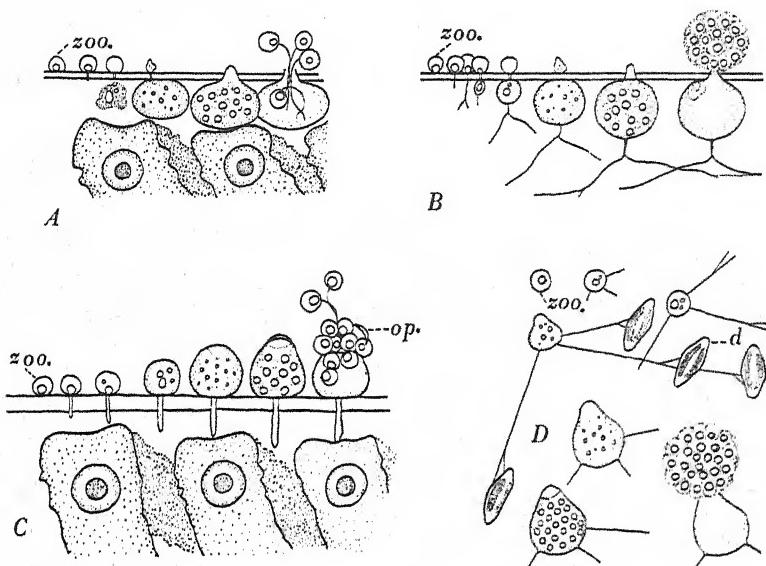


FIG. 1. Diagrams illustrating types of development in chytridiaceous fungi

A. Opidium type: At extreme left an encysted zoospore (*zoo.*) is resting on outer surface of wall of a *Spirogyra* cell; second cyst has produced a penetration tube through which, as shown in third cyst, the contents have been discharged into the host; thallus is enlarging in fourth figure, has become a mature sporangium in the fifth, and is discharging its zoospores in the sixth.

B. Entophyscites type: At extreme left a zoospore (*zoo.*) has encysted on outer surface of wall of an algal cell; second cyst has produced a penetration tube; the third has formed the beginnings of the rhizoidal system; the fourth shows the swelling which will become the reproductive rudiment forming on the very young rhizoidal system; fifth and sixth figures illustrate the further development of the rhizoidal system and of the reproductive rudiment, which has become, in seventh figure, a mature sporangium bearing a discharge tube; last figure on the right shows discharge of the zoospores.

C. Chytridium type: At extreme left a zoospore (*zoo.*) has encysted on outer surface of wall of a *Spirogyra* cell; second cyst has formed a peglike penetration tube, which, in third cyst, has further elongated; contents of cyst remain outside for the most part and, as materials are conveyed to the cyst from the host, its body enlarges, as indicated in third, fourth, and fifth figures, and eventually becomes transformed into a sporangium; in operculate chytrids a well-defined cap or operculum (*op.*) is dehisced, allowing for discharge of the zoospores, whereas in inoperculate chytrids the apex of the sporangium or discharge tube merely deliquesces, as shown in *A*, *B*, and *D*.

D. Rhizidium type:

establishment within the substratum, however, the rhizoids continue to elongate and soon convey materials back through the penetration tube to the persistent epibiotic cyst of the infecting zoospore. As a result, the cyst expands and ultimately becomes the rudiment of the reproductive structure within which all the contents of the vegetative system have been concentrated. This system is then separated from the fertile portion by a cross wall. Although the contents of the cyst are probably partly depleted during the early stages of establishment and growth of the rhizoids, materials soon begin to flow in the opposite direction, and cause the expansion of the reproductive rudiment.

The type of development that occurs in *Phlyctochytrium* and apophysate species of *Chytridium* might be considered here a variation of the *Chytridium* type, although, as has been mentioned, there is equal reason for supposing it to be allied to that found in *Entophyscysis*. In *Phlyctochytrium spp.* and *Chytridium Lagenaria*, for example, an endobiotic subsporangial apophysis is formed which probably always arises as a secondary enlargement of the proximal portion of the already established rudiments of the rhizoidal system. The cyst and the germ tube, however, unlike those in *Entophyscysis* (except *E. bulligera*), remain functional, and, as the endobiotic vegetative system becomes more extensive, materials are carried back to the epibiotic part (Sparrow, 1936a; Karling, 1937c). As a result, the cyst expands, receives the contents of both rhizoids and apophysis, and eventually becomes transformed into a reproductive organ. This alternating intra- and extramatrical habit of development has been termed "endo-exogenous" by Karling (1936a), who considers it an especial characteristic of apophysate chytrids. Since, however, there is necessarily a period during the early stages of penetration

In this type the zoospore (zoo.) usually encysts free in the water, as shown in upper left figure; it then forms one or more rhizoidal outgrowths from its body, as shown in second and third cysts to the right; the cyst expands as material is carried to it by the rhizoids from one or more host cells (*d*), as is clear in succeeding figures, and is eventually converted into a zoosporangium, which, as shown at lower right, discharges its zoospores. All the fungi in Figure 1 illustrate monocentric chytrids, i.e. those in which only one center of reproductive activity (zoosporangium or resting spore) is formed on a single thallus; in the polycentric chytrid more than one reproductive organ forms.

(Sparrow, 1935a)

and establishment of the rhizoids of all epibiotic types during which material is being sent from the cyst into the rhizoids developing in the substratum and none is returned, one should merely say, perhaps, that in these apophysate types this reversal is simply more evident and more striking.

4. *Rhizidium type*.—In the *Rhizidium* type (Fig. 1 D, p. 26) the zoospore comes to rest in the water (or, in exuviae-inhabiting forms, within the hollow substratum) and, after losing its flagellum and encysting, produces one or more rhizoids which radiate from the body. These rhizoids come into contact with and penetrate the substratum. If the fungus is developing in insect exuviae it is possible that the whole surface of the thallus is absorptive. After the rhizoids become established they continue to develop, and materials are conveyed back into the spore body. As a consequence, this structure enlarges and forms the rudiment of either the reproductive organ or, in some genera, the prosporangium. Typically the fertile part of the thallus is not intimately related to the substratum (i.e. it is interbiotic), although occasionally, as in *Polyphagus Euglenae* and *Obelidium*, it may be so. In the majority of genera exhibiting the *Rhizidium* type of development the thallus is monocentric. It is probable that when the development of such polycentric genera as *Physoscladia*, *Nowakowskella*, *Megachytrium*, *Zygochytrium*, *Tetrachytrium*, and the like, is more fully understood, they too will be found to be of the *Rhizidium* type.

In concluding this brief account of development in the chytrids it should be pointed out that much observational and experimental work needs to be done before it can be determined just how static the types really are, however distinctive they may appear under natural conditions. Information is already being accumulated which points to variability in artificial culture. For example, the endobiotic polycentric *Catenaria Anguillulae*, when grown from zoospores sown on artificial media, loses its *Entophyscysts* type of development and approximates a polycentric or even monocentric *Rhizidium* type (J. Bayley Butler and Humphries, 1932).

Structure of the Thallus

As previously indicated, the thallus of the chytrid consists of at least one center of reproductive activity and, with the exception of

the Olpidiaceae, Achlyogotonaceae, and Synchytriaceae, of a more or less well developed nutrient-gathering system (Fig. 1 B, p. 26). In the three families of holocarpic chytrids just mentioned the absorption of materials doubtless occurs over the entire surface of the thallus, which is then converted as a whole into a reproductive organ (Fig. 1 A). The remaining eucarpic chytrids are for the most part "rhizoidal," that is, the purely vegetative part of the thallus consists of unbranched or branched tapering threads or "rhizoids," which are frequently of great delicacy (Fig. 18 A, p. 292). By repeated branching the surface over which, presumably, active absorption of materials occurs is enormously enlarged. In species which form an apophysis (Fig. 10 H-I, p. 152) this surface is still further increased. There is no direct evidence, however, to show that all the endobiotic parts of a chytrid are active in the absorption of materials from the substratum. Sometimes the vegetative system, instead of being rhizoidal, either is cylindrical and blunt-tipped (Fig. 1 C), or is bulbous, coralloid, or composed of short stubby digitations. Such structures are often referred to as "haustoria." In other chytrids, as in *Coenomyces* and *Megachytrium*, the vegetative part is distinctly hypha-like, resembling in this respect the mycelium of the higher fungi. All of these, however, are exceptions to the prevailing rule that the eucarpic chytrids are rhizoidal.

The polycentric thallus¹ is usually far more extensive than the monocentric and is characterized by the formation on it of new centers of thallus organization (Karling, 1932). They are either swellings, which sometimes develop into reproductive structures, or fusiform or ellipsoidal, often septate, purely vegetative "turbinate cells" or "spindle organs." Various conjectures regarding their function have been proposed. It is possible that they serve either to increase the active absorptive surface or, if they become converted wholly or in part into a reproductive structure, to collect materials for the reproductive rudiment. In *Urophlyctis*, an obligate parasite in the tissues of certain phanerogams, similar (but not identical) turbinate cells have been definitely shown to function as vegetative centers from which, after tangential septation, new parts of the extensive thallus originate (Jones and Drechsler, 1920). A like rôle is assigned them by Karling (1931b, 1932), who points out that, in

¹ Karling (1932) called the polycentric thallus a "rhizomycelium," a term which, though useful, carries too great a phylogenetic implication.

Cladochytrium, as the thallus extends its growth, these enlargements serve as successive centers for reduplication or replication of the growing vegetative system.

In most genera of both monocentric and polycentric chytrids the rhizoids are profusely branched. Elongation and further branching may give rise to an extensive vegetative system with an enormous absorptive surface. Branching of the main axes is usually in dichotomous fashion, the diverticula frequently emerging at wide angles. This dichotomy is usually retained in the secondary branches, although there is a marked tendency here toward unequal development of the resulting elements. Thus one secondary branch may remain relatively broad and continue as a main axis, while the other may taper suddenly and terminate its growth. This inequality often brings about the characteristic zigzagging course taken by the main axis as it continues to grow. The individual components of the rhizoidal system may be slightly undulate or unusually straight for long distances. When passing through the walls of the substratum they are sometimes strongly constricted.

Certain chytrids have developed special types of vegetative systems, some of which have been previously mentioned. One of the most curious is the highly flexible extramatrical stalk formed by the diatom parasite *Chytridium versatile*. By its flexibility this needle-like structure which elevates the sporangium above the frustule of the host enables the obpyriform sporangium to bend back as the diatom goes between or pushes against bits of debris commonly present in its environment. After the obstruction is passed the sporangium snaps back to its original upright position (Scherffel, 1926a; Sparrow, 1933a). In genera such as *Rhizosiphon*, *Aphanistis*, *Megachytrium*, *Zygochytrium*, *Tetrahytrium*, and *Coenomyces* the vegetative part of the thallus is more or less isodiametric and blunt-tipped, assuming as a result a distinctly hypha-like aspect. In *Aphanistis* and *Coenomyces* transverse septa are formed. Although these hypha-like filaments strongly resemble those of the higher fungi it is probable that they have no phylogenetic significance and are simply similar vegetative devices occurring in wholly unrelated organisms. Thus they have been repeated in the posteriorly uniflagellate series (*Megachytrium* and others), the anteriorly uniflagellate series (*Hypochytrium*), and the laterally biflagellate series (*Lagenidium*, *Pythium*, and the like).

The walls of the chytrid thallus rarely give a well-marked cellulose reaction with ordinary reagents. Cellulose has, however, been demonstrated in certain species, notably in *Rhizophydium* by Zopf (1887), *Pringsheimiella* by Couch (1939b), and *Rhizophlyctis* by Ward (1939). If it is universally present in the chytrids either the usual methods of demonstrating it are not effective or it is masked by some accessory substance, as in the Monoblepharidales. (See Nabel [1939] for a discussion of the occurrence of chitin and cellulose in the lower fungi.)

In the active vegetative stage the cytoplasm of the chytrid presents a typically lustrous gleaming aspect, and is further characterized by the presence within it of vacuoles, refractive, probably fatty, masses, and minute globules. As the thallus matures changes occur in the cytoplasm. In that of *Obelidium mucronatum*, for example, the globule of the zoospore persists in the homogeneous protoplasm for a time after germination. Eventually it disintegrates, conspicuous vacuoles appear, and the protoplasm of the reproductive rudiment assumes a watery aspect. With the enlargement of the thallus there follows a stage in which the protoplasm is densely and uniformly granular. Minute refractive droplets then make their appearance and, accompanied by a gradual "clearing" of the whole protoplasm, coalesce to form regularly spaced conspicuous refractive globules. During the densely granular stage the delicate rhizoids are completely drained of their contents and a septum is laid down cutting off the sterile and fertile parts of the thallus. Little can be observed of the contents of the rhizoids other than vacuoles in a finely granular matrix and occasional fatty globules.

In most chytrids the cytoplasm and its globules are colorless. In *Polyphagus Euglenae*, *Siphonaria variabilis*, *Rhizoclostratum aurantiacum*, *Cladochytrium replicatum*, *Zygochytrium*, and others, however, in the later stages of maturation, the protoplasm becomes shot through with minute golden or reddish-orange globules. It is these droplets which eventually fuse at maturity to form the regularly spaced colored globules, one in each zoospore. Though in the species cited the pigmented material is found in the globules of the zoospores, in certain others it is retained in the cytoplasm. Sorokin (1874a) found the vivid blue coloration of the cytoplasm of *Tetrachytrium* to be homogeneously dispersed throughout, even after the zoospores were formed. On the other hand, Zopf (1892) noted that the bril-

liant orange hue of the vegetative stage of *Pleotrichelus fulgens* was only temporary, for at maturity the zoospores were colorless. He was probably correct in stating that this coloration was due to the ingested carotene material of the host (*Pilobolus*).

The size of the thallus and, in particular, of the reproductive rudiment formed on it, though falling within certain well-defined limits, is undoubtedly modified somewhat by prevailing external conditions. Of these the most important are probably the availability and nature of food and, in endophytic forms, restrictions of space imposed by the substratum. Competition between individuals of the same or other species may result in the cutting down of both space and nutriment.

REPRODUCTION

Nonsexual Reproduction

In practically all chytrids nonsexual reproduction is accomplished by means of posteriorly uniflagellate zoospores produced in a sporangium which is formed in most instances from the reproductive rudiment of the thallus.

Cleavage of the zoospores.—After the accumulation of protoplasm in the reproductive rudiment and after the sequence of changes previously described the zoospores are delimited. These are usually completely formed, apparently always within the sporangium, by cleavage of the contents into uninucleated segments of similar size. Although delimitation of the spore origins has been described almost uniformly as simultaneous, certain recent observations show beyond question that it is progressive, at least in some species. In *Septopodium lineare* (Sparrow, 1936a), a parasite of diatoms which forms a tubular thallus, progressive cleavage has been observed in living material, not only in the division of the contents into zoospores, but in the formation of the sporangia themselves. Cytological studies of zoospore formation in the polycentric endobiotic *Cladochytrium replicatum* (Karling, 1937b) also reveal a progressive rather than a simultaneous division into zoospores. In sporangia of this fungus, in which the contents are homogeneously distributed throughout, cleavage furrows first appear on the periphery of the mass and extend inward as radial, often somewhat curved arms. The furrows for the most part delimit uninucleate segments. Occasionally, however, bi- and trinucleate segments may first be formed. These, by

the subsequent production of secondary furrows, are ultimately divided into uninucleate "spore initials." The contents of certain sporangia, instead of being uniformly distributed, are disposed around a large vacuole. Such a disposition has been noted in several other chytrids, notably in *Rhizosiphon crassum* (Scherffel, 1926a). In *Cladochytrium replicatum* cleavage furrows appear to originate on the periphery of the vacuole and progress outward as broad wedge-shaped radial arms. Very rarely both methods of cleavage occur in the same sporangium. After delimitation the spore initials become somewhat swollen, possibly because of the intake of water. At this time the contours of the pentagonal, hexagonal, or somewhat cuneiform segments become nearly but not completely obliterated, and the sporangium appears to have just undergone simultaneous division into polyhedral segments. Because of this Karling suggests that the accounts of simultaneous division recorded in the literature are due to the observers' failure to note the early phases, which are actually progressive. The fact that in living material it is usually difficult to follow the process of segmentation has no doubt led to the conflicting accounts of cytokinesis in the chytrids. Cytological observations of this process in numerous representatives of the order are necessary, however, before any sweeping statements can be made.

Obviously the number of zoospores formed in a sporangium is dependent upon the size of the individual spore and of the sporangium. The motile zoospores of a species appear to be relatively constant in size, although most of them are too minute to enable one to obtain any significant measurements. For example, though plants of *Chytridium Lagenaria* when growing on different types of algae ranged from 8 to 29 μ in diameter, the zoospores constantly remained 5 μ (Sparrow, 1936a). On the other hand, the size of the sporangium, as just indicated, may vary considerably in a single species. The factors which influence this are not known with certainty. The nature of the substratum, available space, competition, size of the cell of the substratum (in monophagous types), and available nutrient have been suggested, however, as possible determinants. In a preliminary study of *Chytridium Lagenaria* (Sparrow, *op. cit.*) striking variations in the size of sporangia were noted on three different algae, *Rhizoclonium*, *Spirogyra*, and a slender species of *Oedogonium*. Such variations were not, however, coöordinated with differences in size of the algal cell on which the thallus was develop-

ing. Though the largest sporangia were formed on the alga having the largest cells (*Rhizoclonium*), the smallest were not formed on that with the smallest cells (*Oedogonium*), but, rather, on *Spirogyra*. Evidently in this instance the type of nutrient material or its availability to the fungus was a factor. A similar lack of constant correlation between the size of the sporangia and the cell of the substratum has been observed in other chytrids, notably in *Endochytrium operculatum* (Karling, 1937a). In this fungus mature almost spherical sporangia ranged from 5 to 140 μ and pyriform ones from 5×7 to $60 \times 150 \mu$. Though range in size was to a certain extent proportional to the diameter of the cell of the substratum, small sporangia might be found in large cells or vice versa. *E. operculatum* also demonstrates the variation in the number of zoospores which may be produced by individual sporangia of the same species. Fewer than twenty were found in small sporangia, whereas thousands were estimated to be present in the largest. Haskins (communication) has estimated that up to 70,000 zoospores are formed in large sporangia of *Rhizophlyctis Petersenii* (see also Haskins, 1939).

Discharge of the zoospores.—In inoperculate chytrids there are formed one or more discharge papillae on the sporangium, sometime previous to the cleavage of the zoospores. In certain species these may make their appearance when the thallus is relatively immature. In *Siphonaria variabilis*, to cite an extreme example, the papilla is clearly visible as one of the first-formed elements of the young thallus (Sparrow, 1937a). The degree of development of the papilla varies considerably among the different species. In *Obelidium mucronatum* if a papilla is present at all it must be very slightly developed, since it is not visible at ordinary magnifications on the mature plant (Sparrow, 1938d). In *Rhizophydium sphaerotheca* (Zopf, 1887), *Rhizosiphon crassum* (Scherffel, 1926a), and *Phlyctochytrium chaetiferum* (Karling, 1937c), on the other hand, the papilla is a pronounced and prominent structure. In most of the epibiotic chytrids it protrudes directly from the wall of the sporangium. In others it is slightly elevated, and in *Rhizophydium ampullaceum* (Sorokin, 1874b) it is formed at the tip of a tubular prolongation. The endophytic chytrids for the most part produce a more or less well developed tube which penetrates the wall of the substratum and forms the papilla at its tip. Thus a passageway is made available through which the zoospores are conveyed to the outside me-

dium. This tube may be short, as in *Olpidium Vampyrellae* (Scherffel, 1926a) and *Diplophlyctis laevis* (Sparrow, 1939a), or may attain a considerable length, particularly if it is not so oriented as to gain immediate contact with the wall of the substratum. Its length may vary strikingly in a single species. For example, Karling (1934a) has found in *Catenaria Anguillulae* tubes ranging from 10 to 250 μ in length. It is usual for endophytic types to produce only one tube. *Pleotrichelus fulgens* (Zopf, 1884) offers a notable exception, however, in that it typically forms many tubes. Indeed, it is on this basis that the genus is separated from the predominantly one-tubed *Olpidium*, which it otherwise resembles.

The discharge papilla is characterized by its contents and its strongly arched contour. The contents are ordinarily clear and highly refractive and of an apparently viscid material. At the moment of discharge they may frequently be observed to ooze out into the medium ahead of the emerging zoospores. Just beneath this peripheral zone a clear, less refractive region may often be seen, its concave base in contact with the plasma of the zoospores. At the moment of discharge, however, these two zones appear to become quickly confluent. Whether the materials of the two regions are derived from the wall or from protoplasm of the sporangium it is difficult to say. In species in which a pronounced zonation is apparent, it is possible that the outer, refractive, layer is derived from the wall, the inner, from the contents. Upon dissolution of the papilla a discharge pore is formed through which the zoospores emerge (Fig. 14 E-H, p. 263).

Couch (1932) has observed in *Rhizophydium Couchii* a somewhat different method of discharge-pore formation. In this multiporous species there are formed on the wall from one to five small rounded thin areas. The internal pressure of the expanding spore mass within the sporangium causes the wall to bulge out at these thin spots, which results in the formation of blunt papillae. A similar situation has also been described by Zopf (1887) in the multiporous form called by him "*Rhizophydium pollinis-pini*."

In some species (*Rhizosiphon crassum* Scherffel, 1926b) the wall material of the apex of the tube disappears before discharge, leaving the contents separated from the outside medium by a thin membrane. In certain sporangia of *Diplophlyctis laevis* (Sparrow, 1939a) the outer wall of the tip of the short tube likewise disappears before

discharge. Here, however, a well-defined papilla remains on the surface of the mass of zoospores. This fact might be considered evidence for the cytoplasmic origin of the papilla.

Little can be said with certainty concerning the factors which induce the discharge of the mature sporangia. Under certain conditions they will remain mature but undischarged for relatively long periods, whereas under others they may evacuate their zoospores as soon as they are formed. In general, however, sudden changes in environmental conditions may precipitate sporulation, as in the algae. Thus if sporangia are transferred into fresh clean oxygenated water from the quiet water in which they have matured and which presumably contains various metabolic products accumulated during the vegetative phase of the fungus, discharge can frequently be brought about (Couch, 1939a). Changes in temperature, though most often noted in the literature in connection with the inducing of sporulation in biflagellate Phycomycetes (Coker, 1923), no doubt act in a similar fashion here. There seems to be a certain periodicity in the sporangial discharge of *Phlyctochytrium Hallii* and *P. biporusum* (Couch, 1932), since sporangia of these species have been observed to release their zoospores usually in the late afternoon or evening.

Little is known of the processes within the sporangium which cause the discharge of the zoospores. It is possible that intake of water by the mass of mature spores creates a pressure too great for the modified material of the papilla. If this hypothesis is correct, however, the permeability of the sporangium wall to water must vary, since in undisturbed water sporangia often rest mature and undischarged for some days. Couch (1932) has observed in sporangia of *Phlyctochytrium biporusum* about to discharge that after a period of slight motion the spore initials become quiescent and clear narrow spaces appear between them. This results in the flattening out of those spores next to the wall, as though pressure were being applied to them. Simultaneously the sporangium swells until the wall gives way and discharge of the zoospores is begun. The first spores are ejaculated by internal pressure from within the sporangium, but this soon diminishes in intensity and the remaining swarmers assume individual motility and creep out. Another factor influencing discharge may be the increasing solubility in water, as the sporangium matures, of the material of the papilla. Then, too, some zoospores themselves initiate motility within the sporangium

(J. Bayley Butler and Buckley, 1927), and this motility may have an effect on spore discharge. Whatever the cause, the first zoospores ejected appear, as a rule, to be forced out as if by internal pressure. Later ones, particularly in large sporangia, may creep out amoeboidly or swim out by flagellar action. The rate of emergence has been found in *Catenaria Anguillulae* (J. Bayley Butler and Buckley, *op. cit.*), for example, to vary with each sporangium, irrespective of its size, being highest at the beginning and steadily decreasing as the sporangium empties.

The precise method and the time of formation of the flagellum of the zoospore are not known. Karling (1937b) and Hillegas (1940), who have made perhaps the most extensive cytological study of chytrids, merely state that it is formed while the zoospores are in the sporangium. In many species, for example in *Rhizophydium gonioporum* (Scherffel, 1925b; Sparrow, 1936a), *Phlyctochytrium planicorne*, *P. bullatum*, and *P. dentiferum*, the fully formed flagellum may be clearly seen trailing behind the body of the spore as it emerges. Scherffel (1926a) believes that in *Chytridium Schenkii* the flagellum of the spore is formed after discharge, during the resting period at the orifice of the sporangium. This is denied, however, by Couch (1938b) for the closely allied *C. Oedogonii*, in which, as well as in *R. carpophilum*, the flagellum is coiled in "watch-spring" fashion around the body of the emerged spore and during the rest period merely falls away from the body, straightens, and eventually assumes its activity. This disposition of the flagellum has been noted in other chytrids also (for example, *C. nodulosum*, *C. Schenkii* [Sparrow, 1932b, 1933a]).

The behavior of the emerged zoospores is probably dependent to some degree upon conditions prevailing in the medium at the time of discharge. Under what appear to be excellent conditions they emerge from the sporangium en masse, without flagellar action, and form a motionless group at the sporangial orifice. Here they remain quiescent for a varying period, apparently imbedded in a matrix of mucus or "slime" (Nowakowski, 1876a), which slowly dissolves in the water and liberates them. They then assume flagellar action and swim away either at once or after undergoing a period of collective swarming at or near the orifice of the discharge pore (*Asterophlyctis*, *Siphonaria*, *Rhizidium mycophilum*). Whether the slime is formed from the material of the papilla alone or from the inner wall of the

sporangium or from material between the spore origins (Nowakowski, *op. cit.*), is not known. Observations on certain operculate forms, such as *Nowakowskia elegans* (Sparrow, 1933a) and *Endochytrium operculatum* (Karling, 1937a), indicate that at least part of it is of papillary origin. The formation of a vesicle into which the spores pass upon discharge has been recorded by several workers (Zopf, 1884; Sparrow, 1931c, 1936a, 1937a; Karling, 1937c; and others). Owing to the minuteness of the structures involved, however, and the tenuousness of such membranes, these observations require abundant confirmation.

A further word might be said concerning the remarkable collective swarming which has been noted in certain instances. This phenomenon is perhaps typical of the small group of chytrids inhabiting insect exuviae (Sparrow, 1937a). In *Asterophlyctis* and *Siphonaria* the emerged spores remain for a short time in a motionless cluster at the basal orifice. Then a few on the periphery of the mass initiate individual motion, which ordinarily starts as a slight trembling of each spore body. This increases in intensity and culminates in a violent lashing of the spore from side to side. In a short time all are in motion, and the group becomes a writhing mass of tugging individuals endeavoring to pull their flagella free from some apparently confining substance. After a few minutes of this wild activity, during which the contour of the struggling group may become very elongated, occasional spores dart from the mass. These are quickly followed by others, until all have dispersed. In *Rhizidium mycophilum* (Sparrow, *op. cit.*) the spore behavior is even more extraordinary. After discharge the spores form a compact subspherical mass. Soon they fall apart, and in about a minute each assumes individual movement. Instead of darting away, however, the writhing mass moves about 10μ or more from the orifice and assumes a broadly reniform shape. After several minutes, during which the spores continue to swarm violently and with incredible speed, the shape of the mass changes and becomes broadly sagittate. Finally a few spores dart from the apex of one of the lobes and are soon followed by the remainder, which escape by the same route or from the tip of the opposite lobe. In this type of discharge the spores appear to be beating against a vesicular structure that confines them until they have undergone a period of preliminary "test" swarming.

The significance of this collective swarming, which has been noted in other chytrids as well, is not clear unless it is connected with the

final fashioning of the flagella. It is possible that these are only partly formed at the time of zoospore emergence and may require further maturation before the spore can cope successfully with the outside medium.

Operculate chytrids differ from inoperculate ones in the possession of a more or less convex cap which surmounts the discharge papilla. The operculum is a definite and constant morphological structure in species in which it is formed. For example, all the sporangia on the polycentric thallus of *Nowakowskia* are operculate, and plants grown from zoospores of this plant will form sporangia which in turn will be operculate. There has not as yet been discovered a species of chytrid in which sporangial discharge is at one time inoperculate, at another operculate.

The operculum is probably formed of wall material. At the moment of discharge it is dehisced and either thrown aside or carried up by the mass of emerging zoospores (Fig. 24 B-D, p. 381). Often, as in *Endochytrium ramosum* and *Chytridium perniciosum* (Sparrow, 1933a, 1933c), it appears to be attached hingelike to the orifice. It may be smoothly contoured like a watch glass, with varying degrees of convexity, or may have on its outer surface a pronounced apiculus or umbo. Although in some species (for example, *C. sphaerocarpum*) it is so thin-walled as almost to escape detection, in others it is large and thick-walled, often appearing solid and very conspicuous (as in *C. perniciosum*, *C. olla*). The presence or the absence of an operculum is of great taxonomic importance. Since, unfortunately, one cannot foretell with certainty whether an undischarged sporangium will be operculate or inoperculate, the witnessing of the escape of the zoospores is absolutely essential to proper identification.

Internal proliferation of the sporangium has been indubitably observed in *Cladochytrium*, *Nowakowskia*, and *Physocladia*. This takes place by a renewal of growth and expansion of the presumably nucleated apex of the stalk, which grows up through the floor or base of the previously formed empty sporangium. True internal proliferation, as distinct from mere germination *in situ* of an unescaped swarmer, is still of questionable occurrence in monocentric chytrids.¹ It does occur, beyond question, in the monocentric epibiotic phase of certain species of *Physoderma* (Büsgen, 1887; Clinton, 1902; Sparrow, 1934a).

Structure and behavior of the zoospore.—The zoospore of the chytrid

¹ See *Phlyctochytrium proliferum* Ingold (*Trans. Brit. Mycol. Soc.*, 25:45. 1941).

is a highly characteristic structure, its internal organization being so remarkably uniform throughout the group that an experienced observer of these fungi can recognize it even when it is free-swimming among aquatic debris. The body, which appears to have no well-defined wall, is ordinarily spherical or somewhat ovoid, usually with the broader end posterior. In certain forms, however, it is obovoid (*Rhizophlyctis Mastigotrichis*), cylindrical with rounded ends (*Polyphagus Euglenae*), or rodlike (*Rhizophydiwm goniosporum*). The plasma of the body is generally somewhat lustrous and is homogeneous or bears a few minute refractive granules or contains a globule. A nucleus and a nuclear cap may sometimes be detected, but as a rule these are invisible in the living zoospore. The most conspicuous element in the body is the large refractive globule, which may lie near or at the center (centric), or more often near the periphery (eccentric). Occasionally, as in *Rhizophlyctis Mastigotrichis*, it is basal. The globule is extremely minute in some species, but in others it occupies approximately two thirds of the whole body. A few exceptions to this characteristic internal organization are found. Thus in *Olpidium Vampyrellae* (Scherffel, 1926a) no globule is formed, whereas in *Catenaria Anguillulae* and *Septolpidium lineare* zoospores with several globules are sometimes produced. The latter condition is unusual, however, for in general the type of organization of the zoospore remains relatively constant in a given species.

Various conjectures have been made in the past as to the nature and function of the globule in the zoospore of the chytrid. Early investigators supposed it to be the nucleus, but, probably because of its fatty appearance, soon abandoned this view. Indeed, A. Braun (1856a) himself suggested that it might be oleaginous, and it has since been most commonly referred to as an "oil globule." Microchemical tests by Karling (1937b) indicate that the globule of the zoospore of *Cladochytrium replicatum* is of a more complex nature. Hillegas (1940) has reported similar findings in *Endochytrium operculatum*.

It seems logical to suppose, considering the efficiency of oil as a concentrated source of energy, that the globule provides the material necessary for the activity of the flagellum, and, after encystment, for the production of the penetration tube and the very young thallus. By this means food is assured the developing plant until such time as contact with nutrient materials in the substratum has been estab-

lished. Indeed, early in the formation of the thallus the globule ordinarily fragments and, possibly owing to the resultant increase in surface, is soon absorbed into the cytoplasm.

The posteriorly directed flagellum is attached to the rear of the body in all forms except *Olpidiomorpha* (Scherffel, 1926b) and *Sphaerita* (see p. 79). Preliminary work by Couch (1938c)¹ indicates that with the use of special flagella stains the locomotor organ of certain chytrids may be seen to consist of a long thickened basal part and a thin distal part; this cannot be detected on the living spore or by ordinary staining methods. Although it is known that the flagellum by its rapid vibration propels the spore forward the precise type of motion has not been critically studied. Where it is possible to observe it at all during motility the flagellum is often found to be extended rigidly behind the body, suggesting a pendular rather than an undulating type of vibration. Rapid lateral oscillation of the spore body itself is frequently observed, particularly when motility is first initiated, and the possibility that it may aid in the forward progression should not be overlooked. How the frequent vertical and horizontal changes in direction are effected is not known. It might be conjectured that they are due to changes in the plane of vibration of the flagellum.

The type of movement exhibited by the chytrid zoospore may be either free-swimming or amoeboid, a fact early noted by Schenk (1858b). During swimming the motion may be extremely erratic, the zoospore sometimes hopping and at other times gliding steadily for a while then suddenly going into a series of short convulsive springs. The hopping or dancing type of movement has been considered highly characteristic of the chytrid zoospore, particularly by Scherffel (1925a, 1926b, etc.), but, like the amoeboid type, it is not found in all species. Often the movement may consist solely of extremely rapid darting with frequent pauses and changes of direction; at other times it is a smooth even gliding, accompanied by a gentle rocking or an occasional rotation of the body. During sudden pauses the body may undergo remarkable amoeboid changes of shape and become strongly vacuolate. It then creeps around for varying periods on bits of substrata, its passive flagellum trailing behind. No ingestion of solid materials during such periods has ever been convincingly described. In resuming the swimming type of

¹ See also Couch, *Amer. J. Bot.*, 28:704. 1941.

movement the body of the zoospore all at once becomes rounded, the flagellum vibrates again, and the spore darts off.

The duration of the period of motility of the free-swimming zoospore no doubt depends upon the species of chytrid, the vitality of the individual spore, and the conditions prevailing in the medium at the time. The amount of oxygen, the temperature, and freeness from noxious materials are probably of first importance. Under conditions necessary for observation, from three to four hours is usually a maximum period of swarming, although this is not always true. For example, in *Catenaria Anguillulae*, J. Bayley Butler and Buckley (1927) found that the swarmers remain motile for from fifteen minutes to seven hours. In one remarkable instance (Braun, 1856a) the zoospores of *Rhizophydiump decipiens* continued swarming within the sporangium for one hundred and eight hours.

Not all chytrids possess zoospores capable of pronounced and prolonged motility. Couch (1935a) has reported the flagellated spores of *Phlyctidium anatropum* to be incapable of active swimming. After discharge they merely creep about amoeboidly over objects in the medium, and the flagellum never becomes active. A somewhat similar condition has been noted by Karling (1938c) in *Chytridium aggregatum*. In this fungus the failure of the zoospores to assume motility after emergence from the sporangium results in the characteristic development of clusters of thalli on the surface of the substratum. In the monotypic genera *Amoebochytrium*, *Sporophlyctis*, and *Sporophlyctidium* the spore apparently fails to form a flagellum. In *Amoebochytrium* it shows pronounced amoeboid motion, but in the other genera it either germinates directly in the sporangium (*Sporophlyctis*) or after discharge floats about in the medium (*Sporophlyctidium*), when it is termed an "aplanospore."

Tactic response of the chytrid zoospores to certain external stimuli has been observed. In *Rhizidium vorax* (Strasburger, 1878) and *Polyphagus Euglena* (Nowakowski, in Strasburger, *op. cit.*; Wager, 1913) they have been found to be positively phototactic. Since both of these fungi are parasitic upon motile green algae, the value of this physiological adaptation is readily apparent. The mechanism of the response is not as yet understood. It has been suggested by Wager that in *Polyphagus* the close proximity of the golden globule of the zoospore to the nucleus may indicate that it is a photoreceptive organ. He conjectures that light rays absorbed by it could

cause local changes which, perhaps through the mediation of the nucleus, might exert a directive influence on the free-swimming zoospore. This may possibly be the explanation in *Polyphagus* and certain terrestrial chytrids (Kusano, 1930a), especially since photo-receptive organs are ordinarily pigmented. It would not explain, however, the phototactic response of the zoospore of *Rhizophlyctis vorax*, which has a colorless globule. Furthermore, there are certain well-known chytrids with pigmented globules in their zoospores in which no phototactic response has ever been noted (*Cladochytrium replicatum*, *Rhizoclostratum aurantiacum*, *Siphonaria variabilis*, and so on).

Müller (1911) has observed that the zoospores of *Rhizophyllum pollinis-pini* and of *R. sphaerotheca* are positively chemotactic to genuine protein. The latter fungus also shows a positive response to the products of regressive protein metamorphosis and allied N compounds. The reactions of the swarmers were always greatly inhibited by poisonous materials in the atmosphere and by the lack of oxygen. H and OH ions exerted a negative effect. Similarly, Kusano (1932) has found the swarmers of *Olpidium Trifolii* and *O. Viciae* to be positively chemotactic to juices of their respective phanerogamic hosts. The active substances here were potassium compounds.

It seems probable, then, even from the limited information now available, that the zoospore is greatly aided in seeking out available sources of food in nature by its tactic responses to external stimuli.

Germination of the zoospore.—After the period of swarming the zoospore comes to rest and encysts. During this process the flagellum either contracts and is absorbed into the body or, sometimes, apparently drops off; its precise fate is difficult to follow. At the disappearance of the flagellum the spore body is surrounded by a delicate rigid wall. Further development of the encysted zoospore is dependent upon the proximity of the substratum. If the source of food cannot be reached the spore may degenerate at once or after the formation of a rudimentary rhizoidal system. A curious fusion of zoospores of *Chytridium Lagenaria* in drops of water lacking food has been noted (Sparrow, 1936a). Some of the motile spores settled down in contact with quiescent or even with germinated spores. The contents of the contacting and, by now, encysted spore then flowed into the other one. The receptive body subsequently enlarged, and there ensued during the next five days a remarkable de-

velopment of the rhizoidal system. This was of far greater extent and complexity than that formed by single germinated spores in the same medium. Such unconjugated spores gave rise to only a feebly developed rhizoidal system and disintegrated within twelve hours. It seems probable that this fusion was an attempt by the chytrid to rejuvenate and prolong its vegetative activity under poor nutritional conditions, with the purpose of ultimately reaching a suitable substratum. In connection with these purely morphological observations on vegetative "rejuvenation" by means of the fusion of two protoplasts it is of interest to quote the remarks of Wager (1913) concerning the so-called "double fusion" in *Polyphagus* (see also under "Sexual Reproduction," p. 49): "The double fusion which takes place in the life-cycle of *Polyphagus* is clearly bound up with this dual function of the nucleus, the chromidial fusion in the zygote promoting vegetative growth, whilst the nuclear fusion in the sporangium precedes the formation of the spores. The importation of two nuclei into the zygote appears therefore to be primarily for the purpose of increasing its vegetative activity"

The emergence of a motile swarmer from a cyst has been observed thus far only in *Achlyogeton*, and possibly in *Phlyctidium* (Atkinson, 1894).

Sexual Reproduction

Types of sexuality.—Although much has been learned about the chytrids, particularly in recent years, the sexual reproduction of most species is still unknown; in some chytrids, indeed, such reproduction is suspected of being entirely lacking. It has been established, however, that sexuality when it does exist is of an extremely varied character. In all well-authenticated occurrences the zygote becomes transformed into a resting spore, which upon germination produces swarmers. From this fact it is probable that the thalli are haploid and that the sexually formed resting spore represents the only diploid structure in the life cycle.

In certain species of *Olpidium* which are parasitic upon terrestrial phanerogams (Kusano, 1912, 1929) the fusion of isogamous (like) planogametes (swimming gametes) has been observed (Fig. 2 A, p. 46). After this fusion the biflagellate zygote encysts on the surface of the host, penetrates it, and forms endobiotically a thick-walled resting spore. Among the alga-inhabiting members of the

Olpidiaceae no sexual process has as yet been convincingly demonstrated.

Observations on certain terrestrial chytrids belonging to the genus *Synchytrium* of the Synchytriaceae (Curtis, 1921; Kusano, 1930a) likewise unquestionably show that fusion of isoplano gametes precedes resting-spore formation. Strong, but not conclusive, evidence has been presented by Couch (1931) that a similar type of sexuality also occurs in *Micromyces longispinosus*, an algal parasite belonging to this family.

Sexuality has been noted in one or, possibly, two genera of the Phlyctidiaceae. Gimesi (1924) states that in *Phlyctidium Eudorinae* the resting spore is formed after terminal or lateral fusion of two isogamous gametes, one of which has previously come to rest and germinated. The account and figures of this process are not convincing, and new confirmatory evidence is needed. In several species of *Rhizophydium* a sexual process of a somewhat different nature has been reported (Scherffel, 1925b; Couch, 1932, 1935a; Sparrow, 1933c, 1936a, 1939a). In certain species (as, for example, *R. goniosporum*) the male gamete (rarely two) attaches itself directly to the larger, epibiotic, receptive thallus, which is already established on the host. Communication is made between the two, and the contents of the small encysted male pass into the thallus. There is no loss of identity of the two gametangia, and after the receptive structure, which now contains the two gametes, becomes transformed into a thick-walled resting spore, the empty cyst of the male remains adherent to it. Observations seem to indicate that sometimes, at least, the receptive thallus may undergo considerable enlargement before contact with the male is made. At other times like-sized swarmers settle down in pairs on the surface of the host and establish themselves. One apparently enlarges at a greater rate than the other, receives the contents of the smaller one, and becomes transformed into the resting spore. In *R. Couchii* (Couch, 1932; Sparrow, 1933c) the swarmers which give rise to the gametangia are at first identical in size and shape (Fig. 2 G, p. 46). After a period of swarming they come to rest on the surface of the alga in groups of from four to ten or more. Each of two adjacent encysted swarmers produces an endobiotic rhizoidal system. The epibiotic part of one thallus now enlarges rapidly and continues to extend its rhizoidal system, but the other apparently ceases to grow. Within the larger thallus at

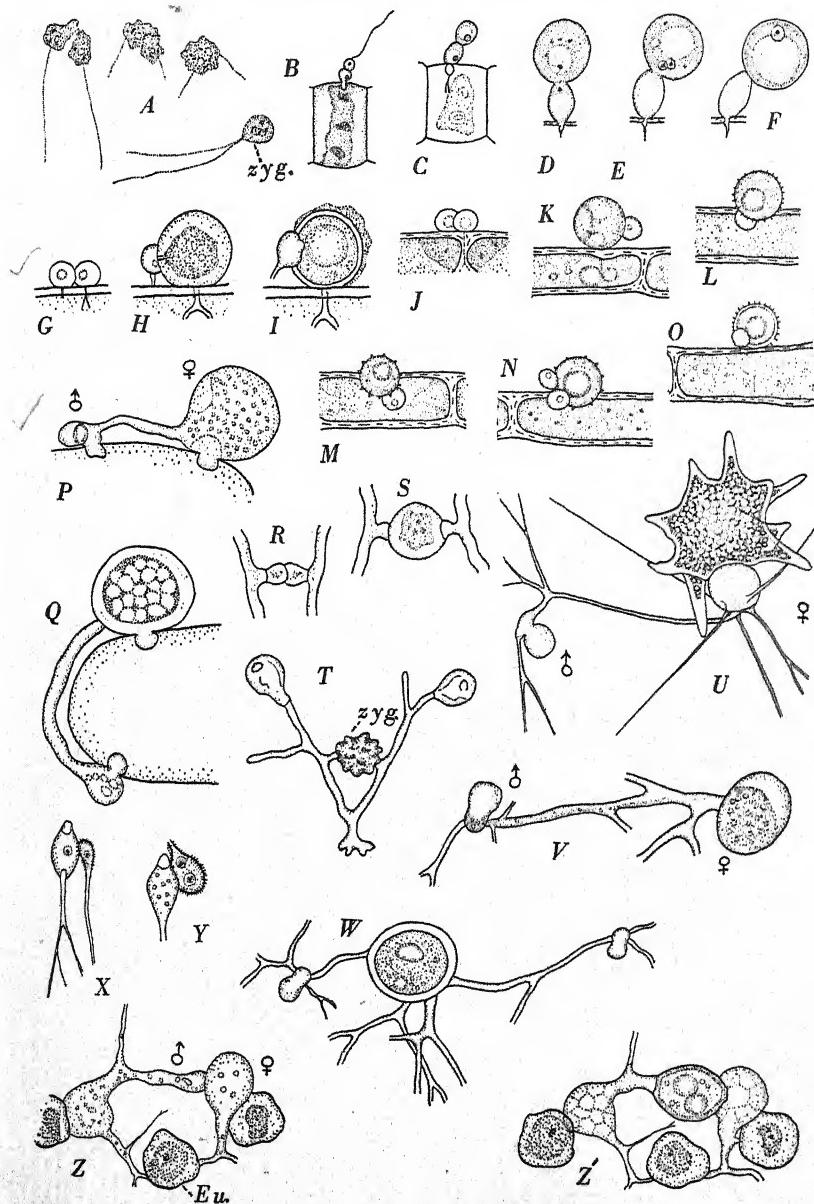


FIG. 2. Sexuality in the Chytridiales

Explanation of Figure 2

A. Stages in conjugation of isogamous planogametes of *Olpidium Trifolii* Schroeter ($\times 600$) (zyg., motile biflagellate zygote). B-F. *Rhizophydi um ovatum* Couch on *Stigeoclonium* (approx. $\times 900$), stages in development of zygote: B, flagellated gamete making contact with young gametangial plant; C-D, gametangia enlarged and stained to show nuclei; E, entrance of gamete of basal gametangium into distal one; F, mature zygote with fusion nucleus and thickened wall. G-I. *Rhizophydi um Couchii*, sp. nov. (approx. $\times 690$), on *Spirogyra* sp., stages in development of zygote: G, two very young gametangia on outer surface of algal wall, with beginnings of rhizoidal systems; H, large receptive gametangium to which is attached small male gametangium; a fertilization tube is clearly visible; I, mature zygote with thickened wall, to which is attached empty male gametangium. J-O. *Rhizophydi um granulosporum* Scherffel ($\times 1000$) on *Tribonema*: J, two very young gametangia on outer surface of algal wall, one with rudimentary rhizoidal system; K, immature zygote with adherent male gametangium; L, more mature zygote bearing echinulations on wall; only the male gametangium appears to have made contact with host; M, similar to preceding but with more peg-like spines; N, immature zygote showing polyandrous condition; O, mature thick-walled zygote; both gametangia have here made contact with host wall. P-Q. *Zygorhizidium Willei* Löwenthal on *Cylindrocystis*: P, large female gametangium and small male gametangium on surface of host cell, connected by a conjugation tube produced by the male; Q, mature thick-walled zygote with male gametangium and tube still attached. R-T. *Zygochytrium aurantiacum* Sorokin (R-S, approx. $\times 335$; T, $\times 300$, according to Sorokin, 1883): R, early stage in conjugation of lateral branches; gametangia are delimited by cross walls; S, immature zygote; T, rough thick-walled mature zygote (zyg.); two empty sporangia are shown at tips of branches. U. Mature zygote of *Asterophlyctis sarcophytoides* H. E. Petersen ($\times 750$) in exuviae, connected by rhizoidal anastomosis to small male gametangium. V-W. *Siphonaria variabilis* H. E. Petersen ($\times 600$) in exuviae: V, large, female, gametangium receiving contents of smaller male through an anastomosed rhizoid; W, mature thick-walled zygote to which are attached two empty male gametangia. X-Y. *Sporophlyctis rostrata* Serbinow on *Draparnaldia*: X, uninucleate gametangia attached laterally; Y, binucleate spiny-walled zygote. Z-Z'. *Polyphagus Euglena* var. *minor* Nowakowski ($\times 400$) on *Euglena* (Eu.): Z, male and female thalli attached by conjugation tube formed by male; Z', later stage of same, showing mature thick-walled zygote which has been formed in distal part of conjugation tube from contents of the two gametangia.

(A, Kusano, 1929; B-F, Couch, 1935a; G-I, Sparrow, 1933c; J-O, Sparrow, 1939a; P-Q, Löwenthal, 1905; R-T, Sorokin, 1874a, 1883; X-Y, Serbinow, 1907)

the point of contact can be observed a short refractive tube seemingly formed by the male gametangium (Fig. 2 H). The entire contents of this gametangium, with the exception of a small globule, is then discharged through the tube into the larger plant, which continues to grow and is ultimately transformed into a thick-walled resting spore to which the empty cyst of the male gametangium—generally torn from its rhizoidal system—remains adherent (Fig. 2 I). In *R. ovatum* (Couch, 1935a) and at times in *R. granulosporum* (Scherffel, 1925b; Sparrow, 1939a) (Fig. 2 J-O) the swarmer which will give rise to the male gametangium comes to rest on the algal cell and forms a rudimentary rhizoidal system. A second, like-sized swarmer then attaches itself to the upper part of this gametangium (Fig. 2 B). The second spore, however, never makes contact with the host and never forms a vegetative system. Eventually it receives the contents of the other gametangium and enlarges to form the resting body. In *R. ovatum*, in which the sequence of development has been carefully followed, both gametangia enlarge at the expense of the host, materials being obtained by the rhizoidal system of the epibiotic male for both it and the more distal receptive thallus. The latter enlarges at a much greater rate and eventually receives the contents of the male thallus through a broad opening formed in the walls at the place of contact. It then becomes converted into a thick-walled smooth resting spore (Fig. 2 C-F). A cytological examination of this process shows the gametangia to be uninucleate and reveals that with the merging of the gametes the nuclei as well as the cytoplasm fuse. A thickened wall is then laid down around the zygote, which is supported at the apex of the thin-walled male gametangium.

It is clear, therefore, that in certain species of the large genus *Rhizophydium* a definite sexual act precedes the formation of the resting spore, although many phases of this process need further amplification. Thus, in none of the observed occurrences is it certain that the swarmer which may form the gametangium is not also capable, if contact is not established with another swarmer, of becoming transformed into a zoosporangium, that is, if it may not be potentially both a zoospore and a gamete. Furthermore, it is not known if the gametes are formed in special gametangia or if from the first they are sexually differentiated as male and female. It is of course possible that in some species a situation similar to that

found in *Synchytrium fulgens* (Kusano, 1930a) prevails. In this chytrid the sex of the gametes is not fixed, the active ones behaving as males and the quiescent or germinated ones as females. Since unfused swarmers may function nonsexually to produce a thallus Kusano feels that they should be regarded as gametes undergoing parthenogenetic development rather than as zoospores. That is, in *S. fulgens* no zoospores are formed, only gametes capable of either sexual fusion or parthenogenetic development. The sexuality of *Rhizophydium* appears to be a step removed from the isogamous planogametic type found in *Olpidium* and closer to the condition in *S. fulgens* in that at least one of the gametes (and sometimes both) is generally nonmotile when contact is established and fusion occurs. It differs from both *Olpidium* and *S. fulgens* in that the swarmers themselves do not fuse. Rather, they give rise after encystment to bodies which contain the gametic material, that is, to gametangia at least one of which has developed a vegetative system and is an immature thallus. Furthermore, even after fusion of the gametes has occurred, the two gametangia remain distinct structures, the one eventually becoming the resting spore, the other, the adherent cyst.

Ledingham (1936) has reported evidence of the occurrence in *Rhizophydium graminis*, a parasite on the roots of certain grasses, of another type of sexuality. In this fungus anastomosis of the rhizoids has been detected, although the actual fusion of the gametes was not witnessed. The same investigator has also reported that fusion of zoospores takes place in *R. graminis*, but he does not describe the fate of these fused swarmers.

Sexuality has been observed in at least five genera of the Rhizidiaceae. In all five the gametic material fuses in elements of one or the other gametangium and is never set free in the medium. Furthermore, in all well-authenticated occurrences the gametangia themselves were more or less mature thalli, often of markedly different size.

The sexual reproduction of the rhizidiaceous *Polyphagus Euglenae* is perhaps the best-known example of this process among the chytrids. The classic investigations of Nowakowski (1876b) on *Polyphagus* showed that one thallus put out a tube which made contact with another (Fig. 2 Z, p. 46). In the more distal part of this tube the contents (gametes) of both thalli accumulated. The zygote then became invested with a thick wall and underwent a period of rest

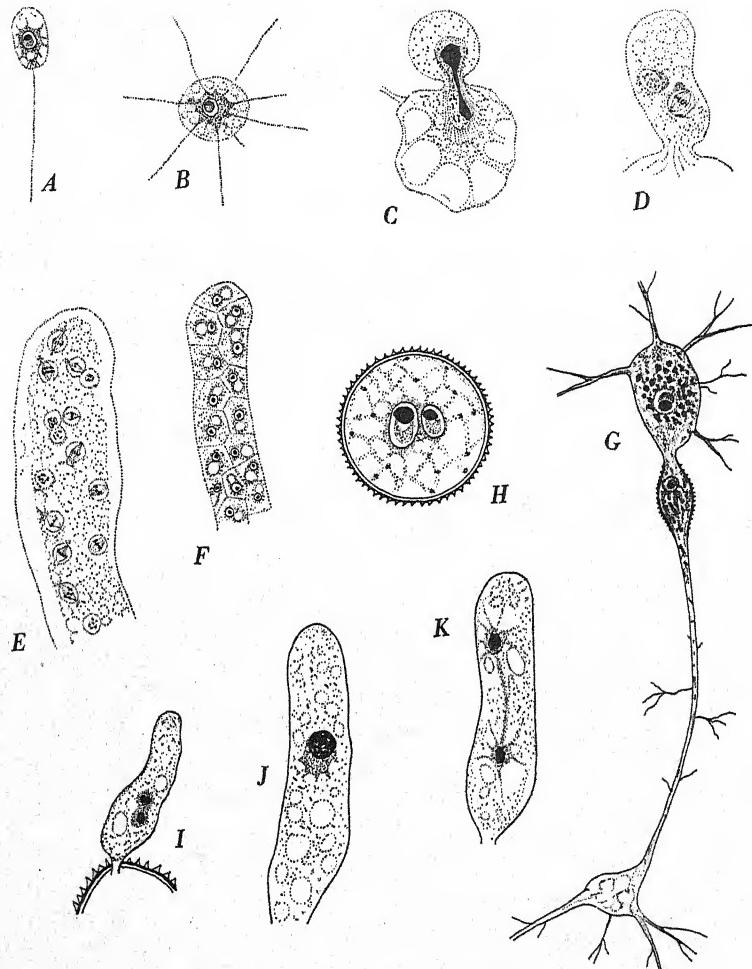


FIG. 3. Cytology of *Polyphagus Euglena* Nowakowski

A. Zoospore with nucleus and basal oil droplet; both oil droplet and nucleus are surrounded by dark-staining chromidial material. B. Young thallus with single nucleus surrounded by chromidial material; delicate rhizoids radiate from periphery of body. C. Single nucleus of large prosporangium passing into smaller, developing sporangium; large nucleolus has been much constricted in passing through the opening. D. Two nuclei in process of division in young sporangium; extruded chromatin lies on periphery of each nucleus; spindle is intranuclear. E. Portion of sporangium

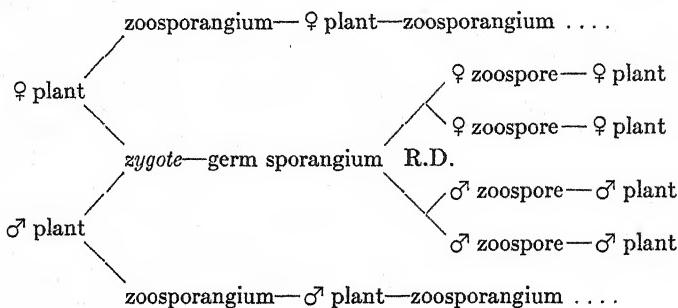
(Fig. 2 Z'). At germination it produced a zoosporangium. Although the tube-producing thallus in *P. Euglenae* is frequently smaller than the other one and is ordinarily referred to as the male, in many individuals there is little or no difference between the two. Indeed, in some instances the male may be the larger. Cytological investigations of this sexual process (Wager, 1899a, 1913; Dangeard, 1900-1901c) show that the two gametes are uninucleate. Wager observed that the male nucleus is the smaller and that it, with the cytoplasm, passes first into the swollen tip of the tube (Fig. 3 G). The female gamete thereupon enters and the two nuclei make contact but do not fuse (Fig. 3 H). The smaller enlarges until it equals the female nucleus in size, and the two move apart to opposite sides of the cell, which is now surrounded by a thick spiny wall. Considerable chromatin is extruded from the nuclei, and as a result they become smaller and show less affinity for stains. The extruded, deep-staining material eventually becomes massed in the center of the cell. At the time of germination the resting spore functions as a prosporangium. There is protruded from its ruptured wall a sphere which increases in size as the contents of the spore emerge into it. The two nuclei pass out into the sporangium (Fig. 3 I) and there fuse (Fig. 3 J). The fusion nucleus then multiplies to form the nuclei of the zoospores, which are eventually cleaved out from the contents.

showing nuclei in process of simultaneous division; at poles of some spindles are kinoplasmic masses with radiating striae. F. Part of sporangium in which zoospores have been delimited; each nucleus bears an oil globule adjacent to it; both globule and nucleus are surrounded by dark-staining chromidial material. G. Two conjugating thalli; male nucleus has already passed into enlarged spiny thick-walled tip of conjugation tube, and larger, female, nucleus is about to do so. H. Spiny resting spore with the two gamete nuclei lying side by side; smaller, male, nucleus soon becomes equal in size to female; later both become smaller, owing to extrusion of chromidia into cytoplasm; deep-stained chromidial material is scattered throughout cytoplasm. I. Developing sporangium, formed at germination of resting spore; the two gamete nuclei have migrated into sporangium and are close together, probably fusing. J. Sporangium formed at germination of resting spore; the two gamete nuclei are now fused. K. Division of large fusion nucleus into two nuclei in sporangium formed by germinating resting spore. (Magnifications not given by Wager, 1913; some figures have been reduced from original.)

(Wager, 1913)

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Although meiosis was not observed it has been supposed to occur at the first division of the fusion nucleus in the sporangium formed by the resting spore (Fig. 3 K). On this hypothesis and proceeding from the fact that in Nowakowski's cultures nearly equal numbers of male and female thalli were formed, Kniep (1928) has proposed that the fungus is dioecious and that the zoospores are sexually differentiated. He suggests (*op. cit.*) the following developmental cycle:



In the closely related *Sporophlyctis*, fusion of two uninucleate thalli of equal size occurs (Serbinow, 1907) (Fig. 2 X, p. 46). Here, one receives through a pore the contents of the other. The distal part of the receptive thallus is then transformed into a thick-walled spiny resting spore (Fig. 2 Y), and fusion of the nuclei follows. The curious sexual reproduction in *Rhizoclosterium*, *Siphonaria*, and *Asterophlyctis* (Fig. 2 U) involves passage of gametic material through anastomosed rhizoids. *Siphonaria* is, however, the only one in which passage of gametic material and fusion have actually been observed (Petersen, 1903; Sparrow, 1937a). Because of the tenuousness of the parts in the remaining genera observations on such processes are difficult even at high magnifications. In *S. variabilis* two (sometimes three) thalli of unequal size make contact by the fusion of elements of their rhizoidal systems. The contents of the smaller plant migrate into the larger one (Fig. 2 V), which then lays down a thick wall around the reproductive rudiment and becomes a resting spore (Fig. 2 W). Active contact of the two thalli appears many times to be accomplished solely by the efforts of the receptive thallus. The rhizoids of this plant seem to seek out the other thallus and often, instead of fusing with some element of the vegetative system, make direct contact with the main body. Whether or not the two types of thalli develop from swarmers formed in the same sporangium is

not known. It has been frequently observed in *Siphonaria*, however, that sporangia of two very different size classes are produced. The cytological aspects of this type of sexual reproduction have not been investigated. It is possible that a similar process precedes resting-spore formation in *Diplophlyctis intestina* (Sparrow, 1936d), although, because of the minuteness of the structures, the evidence is at present inconclusive.

Among the operculate chytrids sexual reproduction has been reported with certainty only in *Zygorhizidium* of the Chytridiaceae and in *Zygochytrium* of the Megachytriaceae. It may possibly occur also in *Tetrahytrium* of the latter family (see pp. 387-390). In *Zygorhizidium* (Löwenthal, 1905; Scherffel, 1925b) epibiotic thalli of different sizes are formed on the algal cell. Each of the smaller thalli produces a tube which makes contact with the lateral wall of a larger plant and fuses with it (Fig. 2 P, p. 46). The contents of the small, "male," thallus are then conveyed into the larger "female," which subsequently becomes transformed into a thick-walled resting spore (Fig. 2 Q). It is probable that upon germination this resting structure produces zoospores. A cytological examination of *Zygorhizidium* by Löwenthal revealed that the two gametangia were uninucleate. The female possessed a relatively large centrally disposed nucleus imbedded in the fatty cytoplasm. That of the male was distinctly smaller. After migration of all or nearly all of the male gametic material a wall was formed which separated the tube from the zygote. Plasmogamy took place at once, but the two nuclei remained separate even after the formation of the thick wall of the resting spore. It is possible that fusion occurs at germination.

Certain aspects of the sexuality of *Zygorhizidium* are puzzling. From the accounts of both Löwenthal and Scherffel two kinds of sporangia are produced, large, "typical," ones about $15\ \mu$ in diameter and "dwarf" ones $4-5.4\ \mu$ in diameter. The latter are considered to be "male" thalli which either have not succeeded in making contact with a receptive plant after forming a conjugation tube or have at once been transformed into sporangia. A further distinction between such sporangia and typical ones, according to Scherffel, is the lack of rhizoids on the endobiotic knob and the failure to produce bending of the host cell. In some specimens at least the "dwarfs" attained nearly the size of the usual sporangia (see Löwenthal, 1905: figs. 17 and 26). Presumably both nonsexual and sexual individuals

have been derived from ordinary zoospores which came from sporangia of typical size. The question arises, then, whether environmental conditions determine the subsequent nature of the thallus formed by the zoospore (nonsexual sporangium or gametangium), or whether there are inherent differences in the swarmers which are produced at the germination of the resting spore. In favor of the former interpretation is the fact (observed by both Löwenthal and Scherffel) that dwarf thalli on which a conjugation tube has already developed may function as sporangia. Since both nonsexual and sexual structures are formed at the same time and since a cytological examination shows that sporangia and receptive thalli of the same size differ in their nuclear condition, the former being multinucleate, the latter uninucleate, the evidence is not conclusive.

The authenticity of Sorokin's account of the sexual process in *Zygochytrium* has long been doubted, as has, indeed, the existence of the genus itself. The type of conjugation appears to be no more aberrant, however, than that found in *Siphonaria* or *Polyphagus*, except that the polycentric *Zygochytrium* is monoecious. According to Sorokin, two short lateral opposing outgrowths are formed, one on each of the main branches of the thallus. The tips of these outgrowths, after fusing, enlarge and, as in a species of *Mucor*, become delimited as like-sized gametangia (Fig. 2 R, p. 46). The contents of the two gametangia then fuse (Fig. 2 S), and from the resulting zygote is formed a thick-walled rough resting spore (Fig. 2 T), which, upon germination, produces in turn a hypha-like structure.

In *Tetrachytrium* fusion of isogamous posteriorly uniflagellate swarmers takes place. The biflagellate zygote does not become transformed into a resting structure, but germinates at once to form a new plant. The behavior of the zygote is so remarkable in *Tetrachytrium*, as compared with all other chytrids, that Sorokin's observations should probably here be regarded with a certain degree of skepticism (Fig. 26 I-M, p. 388).

Couch (1939b) has presented strong but not conclusive evidence to indicate that heterothallism occurs in *Pringsheimiella dioica* and *Rhizophlyctis rosea*. In *Pringsheimiella*, an obligate parasite of *Achlya*, isolated strains when grown alone gave rise only to zoosporangia. When certain strains were paired, however, either with or without actual contact of the hyphae of their respective hosts, abundant resting spores were formed. The type of sexuality involved has evidently not as yet been discovered. With respect to the

saprophytic *R. rosea* the following situation has been observed. Plants of all but one collection were found incapable of forming resting spores. This one collection, however, produced them in abundance. Individual sporangia from it were isolated in separate dishes of sterile water baited with appropriate substrata. Of the twenty monosporangial cultures thus started four showed growth of new plants. In none were resting spores ever formed. When all possible crosses had been made between the four available strains it was found that whenever a certain strain was paired with the others resting spores were produced. It was concluded from this that three of the four strains were of the same "sex," and that the fourth was of the opposite "sex." As in *Pringsheimiella*, the type of sexuality was not determined.

Formation and germination of the resting spore.—The resting spore or "resting sporangium" may be produced either sexually, from the zygote, as previously indicated, or, more often, asexually, from a modified reproductive rudiment or prosporangium or from an apophysis. With the exception of those of *Chytridium* and *Dangeardia*, the asexually developed resting spore is formed either outside or inside the substratum, according to the position of the sporangium. Outstanding features are its thickened wall and its guttulate contents (Fig. 2 I, Q, Z', p. 46). This stout durable wall undoubtedly serves during the rest period to protect the living contents from the harmful, or lethal, effects of unfavorable factors in the environment.

The thallus bearing the asexually formed spore is often indistinguishable at first from that which bears the zoosporangium. As it matures, however, certain distinctive features become evident. For example, the rhizoidal system of monocentric forms is frequently found to be less well developed than that of zoosporangial plants. The contents, particularly those of the reproductive rudiment, become very oleaginous. After the incipient resting spore has attained its maximum size and has received the protoplasm of the rhizoids, its wall begins to thicken. Coincidently the many small globules coalesce, until at maturity a single or, less often, several large ones are formed. The remainder of the contents appears strongly condensed and sometimes may consist of only a relatively thin peripheral layer around the centric or eccentric globule. Since in the formation of the resting spore the contents do not permanently contract, the mature structure usually completely fills its container.

The wall may be smooth or variously ornamented, colorless or

pale yellow to dark brown. In certain smooth-walled types, as for example *Rhizophydium fallax* (Scherffel, 1925b), *R. Couchii* (Couch, 1932), and *Chytridium olla* (de Bary, 1884), it is clearly differentiated into an outer and an inner layer. In these species the outer wall probably represents the wall of the container; the inner, the wall laid down by the accumulated contents of the rudiment. In *C. Lagenaria* (Karling, 1936a), *R. ovatum* (Couch, 1935a), and others the wall is described as consisting of only one layer, and is evidently simply the centripetally thickened wall of the container. Spines, blunt knobs, lobes, undulations, or rays are the most common types of ornamentation. In rough-walled resting spores two distinct layers may generally be discerned, an inner smooth thin one and an outer thicker one which bears the characteristic ornamentation. In the imperfectly known *C. Characii* (Scherffel, *op. cit.*) the outer wall is thick and warty, and clearly prismatic in optical section, as it is in the resting spore of *Blastocladia*, whereas the inner wall is thin and solid. Other curious types of ornamentation are described by Scherffel (*op. cit.*).

The precise method by which ornamentation on the resting spore is produced is not well understood. In *Rhizophydium asterosporum* (Scherffel, 1925b) the incipient and as yet thin-walled resting body forms protrusions which become filled, as the spore matures, with solid refractive often stratified material. In those species of *Rozella* that have a spiny-walled resting spore (Cornu, 1872a; Foust, 1937) the echinulations are described as originating in a clear zone which envelops the densely granular main body. In *Rozella Allomycis* (Foust, *op. cit.*) minute granules appear in the clear enveloping material and align themselves at right angles to the spore wall. They then fuse linearly to form the tenuous spines (Fig. 7, p. 122).

Germination of the resting spores has been observed among representatives of a number of different genera. The factors which induce it are not known with any precision. Generally, as in *Rhizidium mycophilum* (Nowakowski, 1876a) and *Polyphagus Euglenae* (Nowakowski, 1876b; Wager, 1913), a rest period of a month or more appears necessary. Resting spores of *Rhizophydium ovatum* (Couch, 1935a) and *Rhizophydium sp.* (Karling, 1939c), however, may undergo germination in from two to five days after their formation, only a short period of dormancy being required. In by far the majority of instances in which germination has been witnessed the resting struc-

ture functioned as a prosporangium (*Polyphagus*, *Entophyscias*, *Endochytrium*, *Diplophyscias*, *Megachytrium*, *Chytridium*, *Rhizidiopsis*, and *Rhizophydium* sp.). In doing so either the wall of the spore cracked or a pore was formed through which the contents emerged, surrounded by a thin membrane. This structure was converted into a zoosporangium attached to the now empty resting body and discharging its zoospores in the same fashion as the zoosporangium formed on the thallus, that is, either operculately or inopercularly (Fig. 14 C, p. 263; Fig. 16 G, p. 277). Each zoospore gives rise to a new thallus. Direct transformation of the resting spore into a zoosporangium rather than a prosporangium has been occasionally described, notably in *Rhizophydium messanensis* (Morini, 1896), *Rhizophydium transversum* (Dangeard, 1900-1901e), *Rhizophydium ovatum* (Couch, *op. cit.*), *Diplophyscias intestina* (Zopf, 1884), and *Cladophytrium replicatum* (Karling, 1935).¹

The so-called "cyst" formed in *Polyphagus Euglenae* (Dangeard, 1900-1901c; Wager, 1913) is perhaps to be regarded as a less specialized type of resting spore. It is produced simply by the thickening of the wall of the prosporangium and upon germination functions in turn as a typical thin-walled prosporangium.

CYTOTOLOGY

Our knowledge of the cytology of the aquatic chytrids is, except for a few forms, still fragmentary. The most complete accounts we have are those dealing with the interbiotic monocentric *Polyphagus Euglenae* (Wager, 1899a, 1913; Dangeard, 1900-1901c), the endobiotic polycentric *Cladophytrium replicatum* (Karling, 1937b), and the endobiotic monocentric *Endochytrium operculatum* (Hillegas, 1940). Cytological accounts of certain phases of various epibiotic monocentric types have appeared, but since these are all somewhat incomplete they will be discussed under the particular species.

Both Wager and Dangeard are in essential agreement as to the nuclear behavior in *Polyphagus Euglenae*, details of the sexual stage of which have been described above (see under "Sexual Reproduction," p. 49). From Wager's account, the thallus is one-celled and has in the rudiment of the prosporangium a single large more or less spherical nucleus (Fig. 3 B, p. 50). In the resting state this nucleus

¹ See, however, Karling, *Torreya*, 41: 108. 1941.

exhibits a central region of lightly stained meshwork connected by delicate radiating threads to the nuclear membrane. A deeply stained arc-shaped cap lying at one side contains all the chromatin material. Surrounding the nucleus is a coarse densely granular network having a strong affinity for chromatin stains. Deeply staining knots which occur on this reticulum also give a chromatin reaction and are considered to have something to do with oil formation. Whether the precise origin of this so-called "chromidial" net is cytoplasmic or nuclear is not known. It first appears during the later stages in zoospore formation in the sporangium, is present in the young thallus, and passes, finally, along with the nucleus, into the new sporangium, where it becomes dispersed in the cytoplasm. During development chromatin is constantly extruded from the nucleus. After migrating from the mature prosporangium into the enlarging sporangium (Fig. 3 C) the nucleus divides mitotically. The daughter nuclei then continue to divide simultaneously (Fig. 3 D-E) until, in large sporangia, several hundred have been formed. In the mitotic process an intranuclear spindle is formed, on which at the metaphase from ten to twelve minute chromosomes can be observed. Only a small amount of chromatin is used in the production of the chromosomes, the remainder forming a layer on the inner periphery of the nuclear membrane. This layer is visible during the prophases and is ultimately set free in the cytoplasm, where it is used in the growth of the developing sporangium. Soon after the spindle becomes evident the nuclear membrane disappears at the poles, allowing the latter to protrude slightly into the cytoplasm. The remainder of the nuclear membrane then contracts. Centrosome-like bodies are visible at the poles of the spindles at this stage. Upon the separation of the daughter nuclei the nuclear membrane vanishes and the peripheral chromatin mass contracts to form a more or less globular body in the cytoplasm. The chromosomes then become aggregated at the periphery of the new daughter nuclei in contact with a light-staining network which forms the bulk of each new nucleus. Delicate strands persist for a time between the daughter nuclei, but finally disappear.

Nuclear divisions are completed before cytokinesis is initiated. Cleavage lines separating irregular, uninucleated, polyhedral segments of the cytoplasm then make their appearance. In each of the segments the small oil droplets dispersed in the cytoplasm fuse to

form a large globule which is in close contact with the nucleus (Fig. 3 F, p. 50). The deep-staining chromidial mass then appears around both nucleus and globule. At this stage the cleavage planes disappear for a time, to reappear again shortly before discharge. The nucleus of the zoospore is almost centrally located, in close proximity to the globule; the surrounding chromidial mass extends to the point of attachment of the flagellum (Fig. 3 A). Cytological details of the sexual process have already been given (see under "Sexual Reproduction," p. 49).

In the endophytic polycentric *Cladochytrium replicatum* (Karling, 1937b) the infecting zoospore has a large central nucleus (Fig. 4 A, p. 60). Within it is a small nucleolus and, outside the nuclear membrane, a large deeply stained nuclear cap of uncertain origin and composition, similar to that found in *Blastocladia*, *Allomyces*, and *Monoblepharis*. Faint cytoplasmic strands connect the nucleus to the posterior flagellum. After encystment a penetration tube is formed, through which the nucleus and possibly the nuclear cap as well, if this has not already disassociated, pass into the substratum (Fig. 4 B-C). In some individuals the tip of the tube expands at once to form the first turbinate cell, or spindle organ, into which the primary nucleus migrates. In others formation of the first spindle organ may sometimes be delayed until the now strongly elongated nucleus has reached the tip of the tube. Recently migrated nuclei are readily recognized by their distinctly pyriform shape (Fig. 4 D). In them the chromatin forms a faint reticulum and the deeply stained nucleolus is disposed in a broad flat transverse ring around the inner periphery of the narrower end. One or several rhizoids then emerge from the surface of the primary spindle organ and eventually form at their tips new spindle organs. As the primary swelling increases in size the nucleus divides mitotically, with the formation of an intranuclear spindle. During such division the nucleolus persists as a laterally placed, dark-staining, generally arc-shaped structure. Cytokinesis follows, and the spindle organ becomes two-celled. The more distal nucleus subsequently migrates into the secondary rhizoid and eventually comes to lie in the new spindle organ. Sometimes both nuclei migrate from the primary spindle organ before the formation of the septum. The mature thallus thus "replicated" is multi-nucleate, with the nuclei present (save when migrating) only in the spindle organs and rudiments of the reproductive structures. In

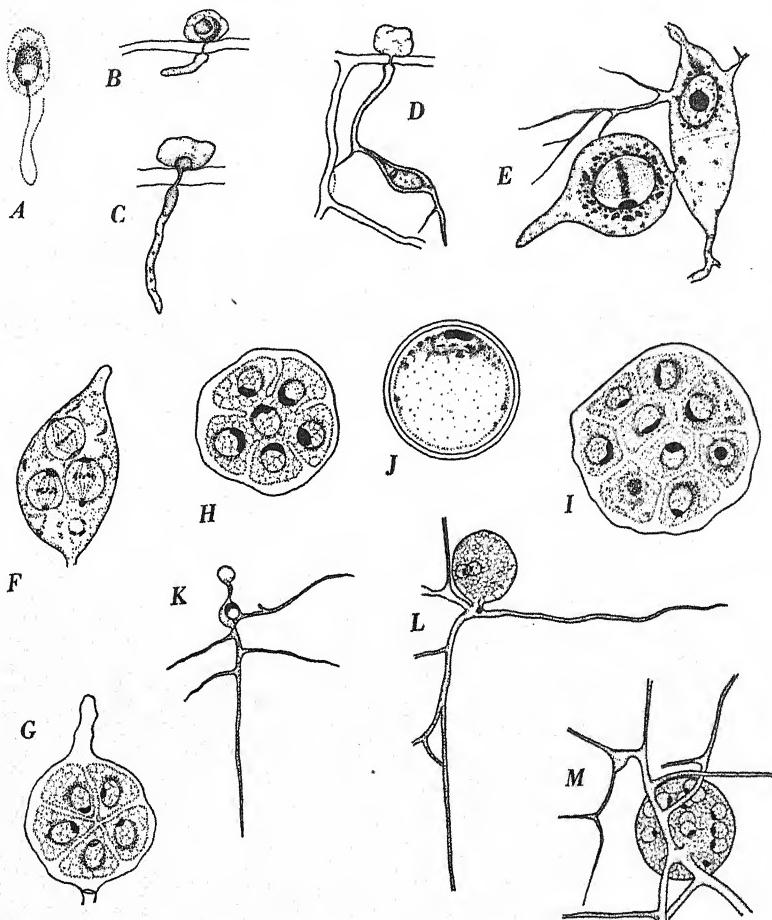


FIG. 4. Cytology of *Cladophytrium replicatum* and *Endochytrium operculatum*

A-J. Cladophytrium replicatum Karling: *A*, zoospore, showing deep-stained nuclear cap over anterior part of nucleus; at opposite pole of nucleus is a small nucleole from which a delicate strand runs to point of attachment of posterior flagellum; *B*, early stage in germination of an encysted spore lying on surface of substratum; *C*, later stage in germination, showing nucleus migrating into germ tube formed within substratum; *D*, pear-shaped primary nucleus resting in first-formed spindle organ; *E*, two-celled spindle organ from one cell of which a zoosporangium is developing; nucleus of zoosporangium is in process of division; persistent nucleole lies within nuclear membrane

the rhizoids the cytoplasm is strongly vacuolate and bears, at irregular intervals, deeply staining granules of unknown composition.

The resting nucleus of the thallus is large and spherical, oval, or citriform. Lying to one side near the inner wall of the nuclear membrane is a conspicuous disclike, oval, or bandlike nucleolus entirely similar to the "chromatin cap" described by Wager (1913) in *Polyphagus*. In addition, a well-defined chromatin reticulum is present and is particularly abundant near the nuclear membrane. The reticulum consists of chromatin granules, net knots, and irregular bodies distributed on a linin framework. The two structures, nucleolus and reticulum, are distinct from each other in appearance, position, and staining properties, a fact which Karling (1937b) believes to argue against the theories of the nucleolar origin of the chromatin. In the spindle organs and the young zoosporangia the nuclei are frequently surrounded by deeply staining granules of unknown origin and nature, strikingly like the "chromidial" material Wager describes in *Polyphagus*. The position of this material makes it impossible to determine with absolute certainty whether or not centrosomes and astral rays are formed.

Various prophase stages have been described by Karling (1937b), to whose paper the reader is referred for further details. It is sufficient to say that the chromatin making up the chromosomes in *Cladochytrium replicatum* does not seem to originate from material extruded or discharged from the nucleolus, as it does in certain terrestrial chytrids (Curtis, 1921; Kusano, 1930a, 1930b; and others), but solely from the contracted chromatin reticulum. The latter, though oriented on the nucleolus, is distinct and separated from it. There are from six to nine chromosomes, the small size of these

(lower side); *F*, longitudinal section of developing zoosporangium in which the three visible nuclei are in equatorial-plate stage of division; *G-I*, sporangia with partly and completely cleaved contents; in *I* masses of densely basophilic granules surround nuclei; *J*, mature resting spore with flattened nucleus lying just beneath wall. *K-M*. *Endochytrium operculatum* (de Wild.) Karling: *K*, young thallus with nucleus in rudiment of endobiotic sporangium; *L*, thallus with two nuclei in sporangial rudiment; what may possibly be extranuclear material is seen at point of attachment of rhizoidal system to sporangial rudiment; *M*, portion of thallus with multinucleate rudiment of zoosporangium; no nuclei were found in the rhizoids.

(*A-J*, Karling, 1937b; *K-M*, Hillegas, 1940)

structures making precise determination of the number difficult. Some reason exists for believing that the division spindle arises from the linin, although the evidence for this is as yet meager. At the time of its formation the nuclear membrane is still very apparent and distinct. The poles of the spindle are centered on two disc-shaped bodies lying on the nuclear membrane. In the metaphase the chromosomes form a crowded ring around the periphery of the equator, the nucleolus persisting as a crescent-shaped dark-staining body at the side of the spindle (Fig. 4 E, p. 60). Actual separation of the individual chromosomes has not been observed, but in the early anaphase the groups of daughter chromosomes form two somewhat flattened loops. Later these turn into more flattened crescentic bands at the poles. The spindle then elongates and penetrates the nuclear membrane, which disappears except at the equatorial region, where it persists for a time. The nucleolus is now liberated into the cytoplasm, where it may remain for a long period before disintegrating and being absorbed. Definite polar radiations appear in the cytoplasm around the chromosome groups. Evidence at present indicates that in the telophase each of the chromosome masses somehow becomes surrounded by a membrane. From each nucleolus-like body the reticulum of the new nucleus then takes its origin. There is nothing to show that the chromosome mass fragments into successively smaller and ultimately dispersed bodies. It is believed that the nucleolus of the new nucleus consists of the residue of the chromosome mass remaining after the reticulum is formed.

Cytokinesis, which occurs after division of the nucleus, appears to be independent of the activity of the achromatic spindle. Actual wall formation in the spindle organs (turbinate cells) is initiated by the formation of a peripheral furrow, which progresses centripetally in the equatorial region. A thin membrane, continuous with the cell wall, extends inward.

The rudiment of the sporangium is uninucleate (Fig. 4 E, p. 60), the nucleus being surrounded (as in *Polyphagus*) by deep-staining material. The number of nuclei is increased by repeated simultaneous mitotic divisions like those occurring in the spindle organs, and, coincidentally, the size of the individual nuclei decreases (Fig. 4 F). The spore origins are cut out by a process of progressive cleavage around the individual nuclei (Fig. 4 G-I). No cytological observations on the nuclear behavior in proliferated sporangia are recorded. The thick-walled asexually formed resting spores (Fig.

4 J) are predominantly uninucleate, although occasional binucleate ones occur.

A cytological investigation by Hillegas (1940) of the monocentric endobiotic *Endochytrium operculatum*, which has an *Entophysycis* type of development, has revealed the following situation: The infecting zoospore differs in no essential features of its internal organization from that of *Cladophytrium replicatum*. After encystment a germ tube is formed which branches and eventually expands locally to produce the incipient zoosporangium. -The nucleus, apparently with the nuclear cap persisting, migrates into the germ tube and comes to lie in the sporangial rudiment (Fig. 4 K, p. 60). Initiation of expansion of the axis to form the rudiment is seemingly not dependent upon the presence of the nucleus in the region, since swelling may take place before nuclear migration. Atypical, binucleate, young thalli are occasionally produced. After the establishment of the nucleated reproductive rudiment and rhizoidal system within the substratum a period of thallus growth ensues which continues until maturity is reached. Meanwhile, the single nucleus, which in the zoospore was less than $2\ \mu$ in diameter, enlarges to $3.5-5\ \mu$, without appreciable alteration in its internal structure. The resting nucleus in the young thallus is essentially like that of *C. replicatum* except that at first no chromatin reticulum can be distinguished. Occasionally, a well-defined nuclear cap is present. While the thallus is expanding, materials are carried back to the reproductive rudiment by the rhizoids. The nucleus, however, remains at all times within the rudiment and just prior to division enlarges to approximately three times its original size. The resting and early prophase stages differ in no respects from those of *C. replicatum*. Nuclear division in the developing sporangium is simultaneous. The spindles are intranuclear, variously oriented, and bear at their poles densely staining conical structures. The latter are considered by Hillegas to function as centrosomes, since prominent astral rays are frequently found radiating from them. The chromosomes were differentiated before the appearance of the achromatic spindle, but because of their small size their number could not be determined. During the metaphase and succeeding division stages the ring-shaped nucleolus persists, although its size and shape may differ in various nuclei. In the anaphase stages the poles of the spindle protrude through the nuclear membrane.

By successive simultaneous divisions numerous nuclei are formed

in the reproductive rudiment; none of them, however, migrates into the rhizoids (Fig. 4 L-M, p. 60). The vegetative system, therefore, is at all stages in its development devoid of nuclei. Progressive cleavage of the contents of the rudiment into zoospores is initiated soon after the protoplasm has become finely granular and homogeneous. The cleavage furrows extend centripetally from the periphery of the contents as well as centrifugally from clefts originating in the mid-region. Apparently there is no central vacuole. The conspicuous nuclear cap of the zoospore appears sometime after the initial stages of cleavage. There is evidence to show that it is wholly of chondriosomal origin. No details of the formation of the flagella or operculum have, presumably, been observed in fixed and stained material.

The resting spore is asexually formed on a thallus similar to that which produces the zoosporangium. The single nucleus (occasionally two) lies in the enlarged rudiment and is surrounded by small heavily staining granules similar to those found in the resting spores of *Polyphagus Euglena* and *Cladophytrium replicatum*. The wall of the mature resting spore consists of an outer thick layer, a thinner middle layer (mesospore), and an innermost thin membranous endospore. The outer wall may occasionally be smooth, but typically it is strongly roughened. During its formation a broad envelope of hyaline gelatinous material of unknown origin surrounds the whole spore. This material shrinks during maturation and becomes transformed at first into broad warts and eventually into lobed processes. Whether these lobes are the result of the infolding of the hyaline material or of outgrowths from the resting spore into the hyaline zone is not known. The wall material, which in the course of its development gave a negative reaction for cellulose, becomes yellowish and opaque. At germination the resting spore functions as a prosporangium. Division of the nucleus, which is mitotic, appears to occur only in the zoosporangium. This structure in most instances rests directly on the empty case of the resting spore, although occasionally it may be produced at the tip of a long tube.

PARASITISM

Before their true nature was understood chytridiaceous fungi were often taken by early investigators to be the reproductive struc-

tures of the aquatic organisms on which they were living. For example, references are found in the early literature to the formation of zoospores by desmids (Archer, 1860), of antherozoids by saprolegnians (Pringsheim, 1860), and of sperms in its eggs by the animal *Nais* (Carter, 1858). Similar misinterpretations might be cited among marine organisms also (Wright, 1879b). As knowledge of Braun's monograph (1856a) became more general, however, the extraneous nature of the chytridiaceous interloper was recognized.

Early observers of these fungi generally assumed that when a chytrid was found on dead or dying algal cells it was the primary causal agent. Rosen (1887) soon pointed out, however, in connection with a study of *Phlyctochytrium Zyg nematis*, that the zoospores of this fungus most often came to rest on obviously dead cells of *Zygnema* or on green filaments which, because of unfavorable environmental conditions, were fast becoming moribund. This saprophytic tendency of chytridiaceous fungi was later emphasized by Serbinow (1907), who, from studies of a number of different chytrid parasites of algae, concluded that many of them were at most only facultative parasites. Serbinow's views have received support from numerous subsequent observations, and it is probable that they hold true for a large number of the Phlyctidiaceae and Chytridiaceae. Certain members of these families appear, however, to be truly parasitic and have never been induced to live saprophytically.

The Chytrid Epidemic

One feature of the chytrids which has been noted by many students of the group is the evanescent nature of their occurrence. Many instances (Cohn, 1853; Zopf, 1888; Dangeard, 1889b; Wager, 1913; and others) are on record of the sudden appearance of these fungi in ponds, as well as in the restricted habitat of the laboratory. Once established, they enjoy a brief period of rapid multiplication, which is followed by a decline, often involving the formation of resting spores, and ultimately by total disappearance. The rapid rate of establishment and the intensity of the epidemic are no doubt due to the virulence of the fungus, as well as to the degree of host-plant susceptibility, which in turn may possibly be strongly influenced by environmental factors. Random samples of collections of algae brought into the laboratory and examined for chytrids may show little or no evidence of their presence. It is a common experience, however, to find that

this material, if left in the laboratory (which is generally warmer than the natural habitat) under conditions which allow for a maximum oxygen supply, will within a few days become infested with various chytrids. At the time of the first examination the invaders may have been present in the water as zoospores, resting spores, or inconspicuous immature thalli. The sudden change in the environment no doubt works to the advantage of the fungi and to the disadvantage of the algae.

The reason for the brief period of rapid multiplication of chytrid individuals once they are established under favorable conditions is readily understandable, as Nowakowski (1876b) long ago indicated for *Polyphagus Euglenae*. The progress of an epidemic of this chytrid can be easily followed in the laboratory. Under favorable conditions a single zoospore, possibly originating in the sporangium formed by a germinating resting spore, will come to rest, germinate, and eventually produce a sporangium within which develop perhaps twenty zoospores. If after the swarmers are liberated only half of them—probably a very low figure—ultimately give rise to new thalli, the first nonsexual generation will have been multiplied tenfold within a short time. At least part of these new thalli will produce new plants and new zoosporangia, and thus enormously increase the number of units capable of causing new infections. Furthermore, in such a form as *Polyphagus*, the effect of this multiplication of individuals on the attacked algae is intensified by the fact that the thalli are strongly polyphagous, each of the tips of the numerous profusely branched and widely spread elements of the rhizoidal system being potentially capable of penetrating a different *Euglena*. In this way the original zoospore has produced a tremendous number of structures able to seek out and infect new host cells, itself and each of its progeny being capable, by means of rhizoids, of invading up to fifty or more *Euglena* individuals. The optimum rate of multiplication does not last long, no doubt being gradually diminished by various adverse factors in the environment, chief of which are probably the shrinking food supply, decrease of oxygen, increase of CO₂, increase of by-products of metabolism, and competition. Natural enemies of the fungus, such as Protozoa which consume the zoospores, develop in the culture, and there appears to be a resistance to attack on the part of a certain percentage of potential host cells. All these factors, as well as others, combine to produce a decline in the number of new

parasites. It is during this period that resting-spore formation often occurs, usually followed by the complete disappearance of the chytrid. Those individuals of the host which have survived the epidemic may then reoccupy the culture, or it may be taken over by other, different, algae. Attempts to maintain these parasitic chytrids in gross cultures are usually unsuccessful, and it even seems that they cannot be induced to reappear, once the epidemic has subsided.

In contrast to such an obligate parasite as *Polyphagus Euglenae*, a great number of chytrids apparently lead a purely saprophytic existence. These forms occur wherever appropriate substrata are available in the natural habitat. Moreover, they readily appear when gross laboratory cultures containing vegetable trash from an aquatic site are "baited" with a variety of organic materials. During the temperate seasons such fungi are probably constantly at work in the submerged decaying parts of plants and animals.

There have also been reported a relatively large number of species which seem capable of living either as saprophytes or parasites (see especially Serbinow, 1907). Unfortunately, it is far easier to demonstrate that a chytrid may live as a saprophyte than it is to prove unquestionably that it can attack a living healthy organism. Saprophytism may be shown, for example, by the simple expedient of boiling the prospective substratum until it is killed and then placing it in a culture dish in which the chytrid is growing. If the fungus attacks this material there is no question of its ability to utilize a dead substratum as a source of food. On the other hand, living microscopic organisms subjected to inoculation experiments must necessarily be taken from their natural environment and placed under more or less restricted and controlled conditions, where the results can be observed. Hence such experiments are handicapped from the beginning, and the significance of the results is definitely limited. It is difficult to judge in successfully induced infection under laboratory conditions whether the virulence of the parasite or the weakened condition of the host made the invasion possible. As has been previously mentioned, changes of environment in all probability bring about changes in the susceptibility of the host. This was early pointed out by Dangeard (1889b), who emphasized that anything which caused impoverishment of the host plant, such as alterations in the properties of the cellulose wall, known to occur under conditions of culture, favored the development of parasites. It should be

recognized in situations where conflicting evidence regarding the parasitism or saprophytism of a species arises that almost never would two investigators be observing the same strain of host and fungus under exactly the same environmental conditions.

Host Specificity

It is commonly found in a mixed collection of algae that only one species of host has been attacked by a particular chytrid. In spite of this, there is little convincing direct evidence to support the view that many of the aquatic chytrids are confined to a single host species or genus. Generalizations in this respect have, however, but slight significance, since relatively little data have thus far been accumulated. A few well-marked instances of apparent host specificity may be cited: Species of *Micromyces* have thus far been found only on conjugates; *Chytridium olla*, with one exception, has been noted only on the oögonia and eggs of *Oedogonium*; *Polyphagus Euglena* primarily attacks quiescent or encysted *Euglena*, although it has also been reported on *Chlamydomonas*; *P. parasiticus* is confined to *Tribonema bombycinum*; *Rhizophydium laterale*, to *Ulothrix*; *Blyttomyces spinulosus*, to the zygotes and zygosporangia of *Spirogyra*; *Podochytrium clavatum*, *R. fusus*, and *Chytridium versatile*, to various diatoms. These are all species which exhibit well-defined distinctive structural features and which do not depend upon the nature of their host for their specific identity. On the other hand, species of *Rozella* and *Olpidium*, which also have apparent host specificities, are poorly defined morphologically, and many of them have been separated from already described species chiefly on the basis of the host. Little or no evidence exists in most instances to support this segregation.

Effect of the Chytrid on the Host Cell

Since parasitic chytrids differ in their effect on the invaded host cell, few generalizations can be made concerning this matter. Almost always, however, except perhaps in Protozoa attacked by certain species of *Sphaerita* and said to extrude the fungus, the invaded host cell is ultimately killed. Braun (1856a:71) noted that whereas chytrid infection produced the death of one-celled algae, it usually killed only the infected cell in multicellular forms. Filaments of multicelled *Ulothrix zonata* infected by *Rhizophydium laterale* were, however, exceptions. In organisms attacked by *Sphaerita* and *Nucleophaga*

(Dangeard, 1889b, 1894-95b) actual death may be delayed for a considerable period after infection, usually until the sporulation of the parasite. It has also been observed that motile chlamydomonads attacked by *R. transversum* may continue to swim about while the thallus of the invader is maturing, and succumb completely only at the time of sporulation of the chytrid.

By reason of their simple body plan, semitransparency, color, and well-defined internal organization, the reaction of green algae to attack by chytrids can frequently be followed with comparative ease. Careful observations on the early stages in the infection of the host have been recorded by several investigators, notably Scherffel and Couch. Scherffel (1925b) records that the first visible reaction of *Tribonema* cells attacked by *Chytridium Confervae* was the concentration of plasma at the point of entrance of the infection tube. The host nucleus was displaced from its central position in the cell and moved to the point of infection. Secretion of wall material then occurred in an attempt to stop the further incursion of the parasite. It was this displacement which suggested to Scherffel the possibility that the nucleus may have a definite rôle in the formation of the wall material. Couch (1932) has described the reactions of the protoplast of *Spirogyra* to the growing rhizoids of the epibiotic *Rhizophyridium Couchii*. Where several young thalli were being formed at one point on the host a violent rotation of the cytoplasm of the alga was apparent, and suggested an attempt to ward off the invading rhizoids. As a result of this activity on the part of the host abnormal development of the rhizoids sometimes ensued. Certain of these rotating cytoplasmic streams communicated directly with the pyrenoids, a fact considered of some significance since it is the stored food material of these pyrenoids which is utilized by the developing fungus. As the course of the infection proceeded, the pyrenoids were destroyed, their starch was hydrolyzed, and the cytoplasmic membrane along with the chloroplasts became contracted and concentrated around the region of the rhizoids. Ultimately disintegration of the whole contents took place.

At times the host is stimulated to abnormal growth, a fact first noted by Braun (1856a:72) in regard to the swelling of *Stigeoclonium* cells infected by *Rhizophyridium mammillatum*. Cells of *Zygogonium* infected by *Micromyces Zygogonii* (Dangeard, 1889b) show a pronounced swelling of the wall. As the fungus develops the deformed

chloroplasts shrink, while the hypertrophy of the wall becomes more pronounced. Eventually the whole contents are consumed, and the reproductive body of the chytrid lies in the distended cell. Infected cells of other conjugates attacked by species of *Micromyces* may at times be bent, swollen, or even burst. An interesting feature of this fungus, and one repeatedly noted, is the strong attraction of the young thallus for the host nucleus. Couch (1931) has intimated the value of this tendency to the fungus, which, by thus achieving a central position in the host cell, is enabled to make contact with the cytoplasmic strands of the alga. Since these are attached to the pyrenoids, the fungus is in an advantageous position for utilizing the reserve food. The young thallus apparently reaches the nucleus either by its own slight amoeboid motion or by cytoplasmic currents of the host. Possibly a tactic response to nucleic acids aids it in making contact with the nucleus. In *Spirogyra* cells attacked by *Micromyces* contraction, disintegration, and discoloration of the chloroplasts gradually take place, and eventually the entire contents are reduced to a granular, often brownish mass within which is imbedded the reproductive structure (prosorus or resting spore) of the chytrid.

In diatoms infected with such epibiotic forms as *Chytridium perniciosum* and *Rhizophyllum fusus* the changes brought about by the invading rhizoids are well marked. Soon after infection the chloroplasts lose their golden-brown color and tend to become yellow green to green. The cytoplasmic membrane contracts somewhat, and the yellow-green chloroplasts become dislocated and eventually fragment. At maturity of the fungus there frequently remain in the frustule only a few chestnut-brown refractive granules.

Perhaps the most unusual and vivid color changes produced by a chytrid are those resulting from infection of *Filarszkya*, a blue-green alga, by *Rhizosiphon crassum* (Scherffel, 1926a). No appreciable change is noted in the infected host cell until the thallus of the fungus is 5-6 μ in diameter. The infected cell as well as adjacent ones then turns deep wine-red, as if the chytrid were producing a poisonous substance which was diffusing through the filament and causing the death of the cells. As the fungous thallus enlarges and the broad absorbing organ invades more and more of the filament, the cross walls are broken down, and new cells become discolored and filled with a clear red-violet or bluish liquid. By this time, the cells

first infected, whose contents have by now been partly or almost wholly exhausted, have turned bright orange and contain light orange-brown granules of unassimilated material. The algal cytoplasm is ultimately consumed save for some residual material, which appears as a series of equidistant broad bands around the absorbing organ of the chytrid.

Wager (1913) has described the sequence of changes occurring in *Euglena* parasitized by *Polyphagus Euglenae*. He observed that discoloration of the chloroplasts occurs soon after infection, the bright green changing to yellow or yellow green. The chloroplast gradually disappears and is replaced by a clump of rusty-red granules. Coincidently with these changes the protoplasm is absorbed, the paramylum grains are broken up, and the granules of the red eye spot are disassociated. The nucleus and cell membrane persist for a time, but the former is gradually absorbed, and after several days the wall disappears, releasing the reddish residual material into the water.

Chytrids are often found parasitizing other aquatic Phycomycetes in old water cultures. If the parasite is endobiotic, as are species of *Rozella*, the hyphae of the host are commonly stimulated to form conspicuous ellipsoidal, spherical, or saclike enlargements. These are frequently isolated from the rest of the hyphae by cross walls apparently produced by the host. Reproductive organs, sporangia, for example, when attacked by such endobiotic parasites retain their general configuration but are usually somewhat enlarged. The protoplasm of infected regions is often strongly vacuolate, or it may contain numerous bodies of fatty material.

Resistance of Algae to Infection by Chytrids

There is no marked evidence to show that healthy algae attacked by chytrids possess varying degrees of immunity. It is frequently observed, however, both in nature and in gross cultures, that during the progress of an epidemic certain individuals of a species remain uninvaded. Whether this is due to inherent factors within the alga (general health, vigor, state of the cellulose wall, and so on) or to external conditions is not known.

The attempts of some algae to ward off attack by chytrids by what might be termed "mechanical means," that is, by "protective plugs" of wall material, have been observed in numerous instances. This

curious method of defense was early noted by Braun (1856a) in *Ulothrix zonata* attacked by *Rhizophydium laterale* and has since been found in other members of the Chlorophyceae and in Heterokontae, as well as in the phycomycete *Allomyces* (Scherffel, 1925b; Dangeard, 1937; Foust, 1937; Couch, 1938b; Sparrow, 1939a). Certain flowering plants react in a similar manner when attacked by chytrid zoospores (see especially Kusano, 1936). The formation and functioning of these protective plugs or calluses have been described at some length by Dangeard in vigorous individuals of *Closterium Ehrenbergii* attacked by *Phlyctochytrium Desmidacearum*. In this instance the zoospore of the chytrid, after encysting on the surface of the host, produced a delicate tube which penetrated the algal wall in its effort to make contact with the living cytoplasmic membrane. It was found, however, that in the short period during which penetration was taking place the host had responded to the incursion by the formation of a sheath of wall material which surrounded the infection tube. As the latter elongated, the sheath too became extended, at all times insulating, as it were, the fungus from the living cytoplasm of the alga. During this process of elongation the chytrid germling was necessarily using up its own food supply in an effort to reach the nutritive contents of the alga. The chytrid, with no nourishment forthcoming and its own supply exhausted by the tube formation, was literally "starved out." But Dangeard also noted that when host cells were growing under unfavorable conditions or when they had been weakened by the attacks of other parasites they lacked this capacity for callus formation and succumbed in great numbers to the chytrid.

Hyperparasitism

Instances of one chytrid parasitizing another have been noted occasionally by various investigators. Serbinow (1907) has recorded the invasion of the prosporangia of *Saccommyses* by another chytrid, called by him "*Phlyctidium Dangeardii*." No endobiotic system was found and it is possible that he was dealing with a species of *Rozella* parasitic in the sporangium rather than in the prosporangium of the host. Sporangia of the marine species *Rhizophydium discinctum* and *Chytridium Polysiphoniae* have been found to be attacked by other chytrids, the first by *Pleotrichelus paradoxus* (H. E. Petersen, 1905) and the second by *Rozella marina* (Sparrow, 1936b).

Similarly, sporangia of the fresh-water *Rhizophydium goniosporum* and *Phlyctidium Bumilleriae* have been invaded by *Rhizophydium parasitans* (Scherffel, 1925b) and *Phlyctidium anomalum* (Couch, 1932), respectively. Prosporangia of *Polyphagus Euglenae* have been known to be attacked by a species of *Rozella* (*R. Polyphagi* Sparrow, 1936a).

SYSTEMATIC ACCOUNT

CHYTRIDIALES

MICROSCOPIC parasitic or saprophytic primarily aquatic fungi of simple body plan, the thallus either endobiotic, without specialized vegetative structures and converted as a whole (holocarpic) into one or more reproductive organs, or epi-, endo-, or interbiotic or extramatrical and differentiated into a more or less extensive unbranched or branched, generally nonseptate rhizoidal (rarely tubular and septate) vegetative system, at least the tips of which in interbiotic and extramatrical forms are endobiotic, and one (monocentric) or more (polycentric) reproductive organs (eucarpic); contents refractive with glistening globules and minute granules, walls occasionally giving a cellulose reaction; zoosporangia discharging after the deliquescence or rupturing of one or more papillae (inoperculate) or after the dehiscence of an operculum (operculate), zoospores generally formed within the sporangium, posteriorly uniflagellate (flagella lacking in several genera), usually bearing a conspicuous oil globule, movement hopping or swimming or amoeboid, encysting before penetration; resting spore thick-walled, generally filling its container, often with a large globule, asexually formed or sexually after fusion of isogamous planogametes or anisogamous aplanogametes borne in thalloid gametangia, upon germination functioning as a zoosporangium or prosporangium.

Occurring on a wide variety of fresh-water algae, as well as on fresh-water fungi, pollen grains, decaying plant tissues, and microscopic animals. A very few found in marine waters on seaweeds. Some species of primarily aquatic genera and the species of *Synchy-*

trium and *Physoderma* (including *Urophlyctis*) occur as obligate parasites of terrestrial flowering plants.

The order as defined here is restricted to "chytrids" with posteriorly uniflagellate zoospores formed in the sporangium. There are recognizable within the group two parallel series in which specialization of the thallus has achieved equal complexity; in one the sporangium opens by the deliquescence or rupturing of the tip of the discharge tube (Inoperculatae), in the other, by the dehiscence of a very definite and discrete operculum (Operculatae).

KEY TO THE FAMILIES OF THE CHYTRIDIALES

- Sporangium opening by the deliquescence or rupturing of one or more papillae Series INOPERCULATAE, p. 75
- Thallus holocarpic, without specialized vegetative structures, endobiotic
 - Thallus forming a single sporangium OLPIIDIACEAE, p. 75
 - Thallus forming more than one sporangium
 - Thallus converted into a linear series of sporangia
 - ACHLYOGETONACEAE, p. 128
 - Thallus converted into a prosorus or sorus surrounded by a common soral membrane SYNCHYTRIACEAE, p. 135
- Thallus eucarpic, i.e. differentiated into a vegetative system and reproductive organs, monocentric or polycentric, epi- and endobiotic, endobiotic, interbiotic, or extramatrical
 - Thallus always monocentric
 - Thallus epi- and endobiotic, or entirely endobiotic, reproductive organ epi- or endobiotic PHLYCTIDIACEAE, p. 143
 - Thallus interbiotic; sporangium, prosporangium, or resting spore formed from the enlarged body of the encysted zoospore RHIZIDIACEAE, p. 271
 - Thallus, at least in some phases, polycentric
 - Sporangia and resting spores formed on the same endobiotic polycentric thallus CLADOCHYTRIACEAE, p. 304
 - [Sporangia and resting spores formed on separate thalli; sporangia epibiotic, thallus monocentric; resting spores endobiotic, thallus polycentric..... PHYSODERMATACEAE¹]
- Sporangium opening by the dehiscence of an operculum
 - Series OPERCULATAE, p. 323

¹ The Physodermataceae are primarily parasites of terrestrial phanerogams and are not included here (see p. 304).

Thallus monocentric, epi- and endobiotic, or endobiotic

CHYTRIDIACEAE, p. 323

Thallus polycentric, completely endobiotic, or endobiotic and extramatrical MEGACHYTRIACEAE, p. 378

INOPERCULATAE

OLPIDIACEAE

Thallus endobiotic, holocarpic, without a specialized vegetative system, converted as a whole into a single inoperculate sporangium or a resting spore; zoospores formed in the sporangium, posteriorly uniflagellate, generally with a single globule; sexuality, where known, by fusion of posteriorly uniflagellate planogametes, the zygote after penetration forming an endobiotic resting spore which upon germination functions as a zoosporangium.

A large primarily aquatic family, the members of which are found as parasites and saprophytes of fresh-water algae, fresh-water and marine Phycomycetes, microscopic animals, and plant spores. Several species are also known as parasites of flowering plants, notably *Olpidium Brassicae* (Woronin) Dang. (see Woronin, 1878:557), *O. Viciae* Kusano (1912), *O. Trifolii* Schroeter (see Kusano, 1929), *O. Agrostidis* Sampson (1932).

Undoubted instances of a sexual act preceding resting-spore formation have been found by Kusano in *Olpidium Viciae* and *O. Trifolii* and by Sawada (1922) in *O. Bothriospermii*. See under *Olpidium*, page 83.

KEY TO THE GENERA OF THE OLPIDIACEAE

Zoospore with the flagellum subapically attached, the body bearing an anterior ring of refractive granules OLPIDIOMORPHA, p. 76

Zoospore with the flagellum posteriorly attached (except in *Sphaerita*), the body generally bearing a single prominent globule

Sporangium never filling the host cell, with a very short discharge papilla or devoid of a specialized discharge apparatus; the wall simply bursting at maturity; parasitic in Euglenophyta or amoebae

Parasitic in the nuclei of amoebae NUCLEOPHAGA, p. 77
Parasitic in the protoplasm of Euglenophyta and amoebae

SPHAERITA, p. 79

- Sporangium not filling or filling the host cell, with one or more well-defined discharge tubes; parasitic in algae, fungi, or microscopic animals
- Sporangium more or less ovoid, spherical, or tubular, never completely filling the host cell or losing its individuality
- Sporangium with one (rarely more) discharge tube
- Sporangia generally scattered; resting spore not resting loosely in a container..... *OLPIDIUM*, p. 82
- Sporangia formed in dense clusters; resting spore resting loosely in a container..... *PRINGSHEIMIELLA*, p. 108
- Sporangium predominantly with numerous discharge tubes
- PLEOTRACHELUS, p. 109
- Sporangium more or less completely filling the host cell and assuming its shape
- Sporangium nearly filling the host cell; its walls, however, never completing fusing with those of the host
- PLASMOPHAGUS, p. 115
- Sporangium completely filling the reproductive organ or hypertrophied part of the host; the walls of host and parasite fused, at least laterally *ROZELLA*, p. 116

OLPIDIOMORPHA SCHERFFEL

Arch. Protistenk., 54:515. 1926

(Figure 5J, p. 78)

Thallus endobiotic, holocarpic, resembling *Olpidium*; contents refractive, with glistening irregular lumps but without fat globules; sporangium inoperculate, with a single discharge tube; zoospores formed within the sporangium, emerging upon the dissolution of the tip of the discharge tube, with a single trailing lateral subapically attached flagellum, the body containing an anterior ring of refractive granules; resting spore not observed.

Differing from *Olpidium* in the structure of the zoospore and, to a lesser degree, in the lack of the characteristic chytridiaceous fat globules in the contents of the developing sporangium.

OLPIDIOMORPHA PSEUDOSPORAE Scherffel

Arch. Protistenk., 54:515, pl. 28, figs. 7-8. 1926

Sporangium more or less spherical or broadly ovoid, 8-14 μ in diameter, with a single long slender discharge tube 3 μ in diameter,

wall thin, smooth, colorless; zoospores ovoid, $3\text{--}4 \mu$ long by 2μ in diameter, slightly attenuated posteriorly, plasma dense, homogeneous, with an anterior circlet of strongly refractive granules and a small lateral basal vacuole, flagellum from four to five times as long as body, emerging individually and at once swimming away, movement smooth, gliding in a zigzag line; resting spores not observed.

In zoocyst of *Pseudospora leptoderma*, living in *Vaucheria* sp., HUNGARY.

NUCLEOPHAGA DANGEARD

Le Botaniste, 4:214. 1894-95

(Figure 5 A, p. 78)

Thallus endobiotic, within the nucleus of the host, holocarpic; sporangium inoperculate, formed from the walled thallus, filling the nuclear cavity, spores simultaneously formed, set free upon the disintegration of the host body.

A genus of uncertain relationships.

NUCLEOPHAGA AMOEBAE Dangeard

Le Botaniste, 4:214, figs. 1-5. 1894-95

From one to five sporangia in the hypertrophied nucleus of the amoeba; spores spherical, up to one hundred in a sporangium.

In *Amoeba verrucosa*, FRANCE.

Since the vegetative body of the organism did not ingest the solid particles of the host Dangeard considered *Nucleophaga Amoebae* a chytrid allied to *Sphaerita*. The vital activities of the host were not affected until the time of sporulation of the parasite. The host then disintegrated, allowing the spores to be dispersed.

A *Nucleophaga* sp. has also been reported by Scherffel (1902a) in *Zygnema*. Numerous records occur in the extensive protozoological literature (see Sassuchin, 1934; Brumpt and Lavier, 1935).

Doflein (1907) has described motile bodies in a parasite of *Amoeba* which conjugate to form biflagellate zygotes. There is no real evidence that they belong to Dangeard's fungus, particularly since the flagellum is said to be anterior.

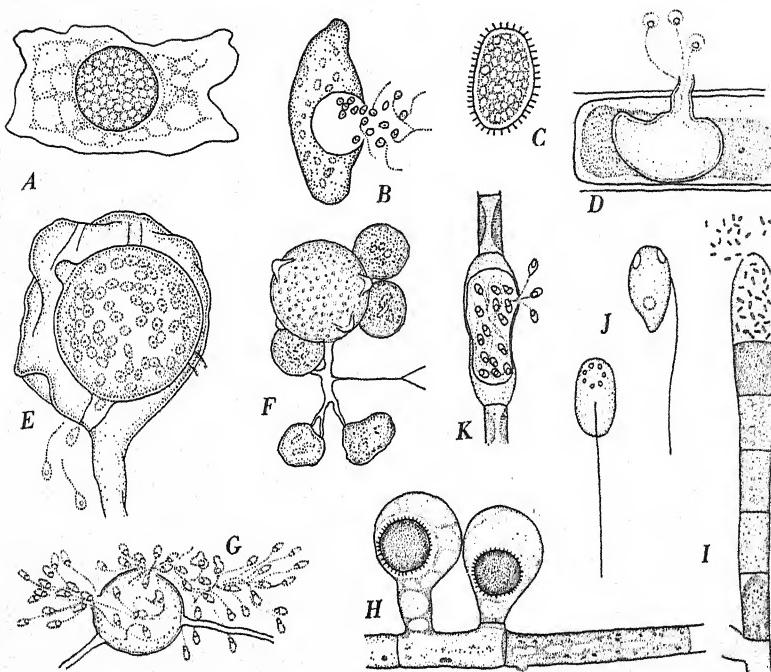


FIG. 5. Olpidiaceae

A. *Nucleophaga Amoebae* Dangeard in *Amoeba*, mature sporangium in nucleus of *A. verrucosa*. B-C. *Sphaerita Dangeardii* Chatton and Brodsky in *Euglena*: B, sporangium discharging its spores to outside of host; C, thick-walled spiny resting spore. D. Sporangium of *Olpidium endogenum* (Braun) Schroeter ($\times 400$) in cell of *Zygnema*, with last of zoospores just emerging. E. *Pleotrichelus fulgens* Zopf ($\times 450$) in *Pilobolus*, discharging sporangium. F-G. *Rozella Polyphagi* Sparrow ($\times 550$) in prosporangium of *Polyphagus Euglenae*: F, mature sporangium, with several discharge papillae, completely filling parasitized prosporangium of host; G, discharge of zoospores. H-I. *Rozella septigena* Cornu in hyphae of *Achlya* and *Saprolegnia*: H, resting spores ($\times 250$) in swollen lateral hyphal outgrowths of *Saprolegnia spiralis*; at right is young zoosporangium of parasite with a discharge papilla; around left-hand resting spore the hyaline region, within which spines are formed, still persists; I, portion of hypha of *Achlya polyandra*, showing sporangia of *Rozella septigena* ($\times 125$) in various stages of development; in lowest segment wall of parasite has not yet fused with that of host; at the tip the sporangium is discharging its zoospores; in third cell from the top the strongly vacuolate stage of the protoplasm is shown. J

SPHAERITA DANGEARD

Bull. Soc. Bot. France, 33:241. 1886; Ann. Sci. Nat. Bot.,
VII, 4:277. 1886
(Figure 5 B-C)

Thallus parasitic in the cytoplasm of Rhizopoda and Euglenophyta, endobiotic, holocarpic, walled, without specialized vegetative structures, forming the rudiment of the sporangium; sporangium inoperculate, spherical, ellipsoidal or fusiform, usually liberated from the host at maturity, discharging its zoospores by a splitting of the wall or by the formation of a discharge papilla; zoospores uniflagellate, the flagellum anteriorly attached but directed posteriorly; resting spores not known with certainty.

Species of *Sphaerita* are all parasitic in the cytoplasm of the host, on which they may often exert little effect, at least until the sporulation of the parasite, when death may ensue.

Dangeard (1933) has recently indicated that in view of the fact that *Sphaerita Dangeardii*, a species parasitic in *Euglena*, has been more adequately studied than his *S. endogena* he would designate it, if this does not violate the rules of nomenclature, as the type of the genus. He feels that further investigations of *S. endogena* in Rhizopoda may indicate that it should be segregated in a genus of its own. Indeed, it might be pointed out that under Article 64 of the International Rules the specific name *endogena* should be discarded as a *nomen confusum*.

Dangeard (1933) also states that the spiny resting spores described (1889b:46) for *Sphaerita endogena* in *Euglena* may actually belong to *S. Dangeardii* and that the conjugation of zoospores observed (1889b:49, pl. 3, fig. 8), later ascribed to incomplete segmentation, was indeed a sexual process similar to that found in *Olpidium Viciae*. In his earlier researches Dangeard did not recognize that at least two different parasites might be present in the *Euglena*, one with uni-

Olpidiomorpha Pseudosporae Scherffel ($\times 1000$), zoospores, showing subapical attachment of flagellum and anterior refractive granules. *K. Plasmophagus Oedogoniorum* de Wildeman ($\times 600$), discharging sporangium in *Tribonema*.

(A, Dangeard, 1894-95b; B-C, Dangeard, 1889b; D, F-G, Sparrow, 1936a; E, Zopf, 1884; H-I, Cornu, 1872a; J, Scherffel, 1926b; K, Sparrow, 1933c)

flagellate zoospores (*Sphaerita*) and another with biflagellate zoospores (*Pseudosphaerita*). This, together with the fact that data were often obtained from fixed material, has led to much confusion in distinguishing what structures belong to a particular fungus. The following treatment is probably only partly successful in unraveling the tangle, since new observations alone can solve it. Many references to "*Sphaerita*" may be found in protozoological literature, but little can be got from them since they ordinarily refer only to fixed and stained material. See also *Pseudosphaerita*, page 638.

SPHAERITA DANGEARDII Chatton and Brodsky

Arch. Protistenk., 17:8. 1909

(Figure 5 B-C, p. 78)

Sphaerita endogena Dangeard, pro parte (in *Euglena*), Ann. Sci. Nat. Bot., VII, 4:277, pl. 12, figs. 14-21. 1886.

Sporangium spherical or somewhat ellipsoidal, extremely thin-walled, sometimes with two oppositely placed short discharge papillae; zoospores spherical or ovoid, 1.5-2 μ in diameter, resting for a short time after discharge, movement hopping or slightly amoeboid; resting spore (?) ovoid, 12 μ long by 8 μ in diameter, with a brownish spiny wall, upon germination forming a discharge papilla and functioning as a zoosporangium.

Parasitic in *Euglenid spp.*, Dangeard (*loc. cit.*; 1889b:46, pl. 2, figs. 11-19, pl. 3, figs. 1-2), FRANCE; *Euglena sp.*, Constantineanu (1901:370), RUMANIA; *Euglena sp.*, Serbinow (1907:154, pl. 5, figs. 4-8), RUSSIA; *Euglena viridis*, Valkanov (1931a:361), BULGARIA.

No statement is made by Dangeard (1933) as to whether the *Sphaerita* in *Phacus* and *Trachelomonas* is to be considered here or in *S. endogena*. Whether or not the smooth-walled resting spores described in the 1886 paper belong here is apparently not known.

IMPERFECTLY KNOWN SPECIES OF SPHAERITA

? **SPHAERITA ENDOGENA** Dangeard

Pro parte (in *Rhizopoda*), Ann. Sci. Nat. Bot., VII, 4:277, pl. 12, figs. 22-36. 1886

Sporangia single or in groups, spherical or somewhat elongate, 5-20 μ in diameter, the spores when mature appearing as mulberry-

like masses, expelled from the host at maturity and liberated by rupturing of the wall, apparently without flagella; resting stage not observed.

Parasitic in Rhizopoda, *Nuclearia simplex*, and *Heterophrys dispersa*, Dangeard (*loc. cit.*), *Amoeba limax*, Chatton and Brodsky (1909:3, figs. 1-3), FRANCE; *Nuclearia simplex*, Constantineanu (1901:370), RUMANIA.

Records of the occurrence of *Sphaerita endogena* and other "species" in parasitic amoebae are frequent in the protozoological literature. No attempt has been made to collect or evaluate the descriptions of these organisms. Many descriptions have been derived from a study of fixed and stained material only and are of little value from a morphological standpoint.

Chatton and Brodsky have emphasized that characteristically the very young thallus has an eccentric nucleus apparently without a membrane. Their studies on fixed and stained material indicated that the thallus is surrounded at all times by a wall, that the nuclei divide simultaneously, and that the spores are formed by condensation of the cytoplasm around each of the nuclei. Secretion of a thin wall follows. The spores were liberated simply by the rupturing of the wall, no special discharge pore being formed. These investigators noted, as did Dangeard, that the liberated spores of *Sphaerita endogena* parasitizing Rhizopoda lacked motility. Dangeard later (1933) emphasizes this point as indicative of a specific and perhaps even a generic difference between *S. endogena* and the parasite of *Euglena* (*S. Dangeardii*).

? SPHAERITA TRACHELOMONADIS Skvortzow

Arch. Protistenk., 57:205, fig. 2. 1927

Sporangium broadly ellipsoidal, with broad rounded ends, 20-29 μ long by 18-20 μ in diameter, wall thin, smooth; zoospores not observed; resting spore spherical, with a thick brownish spiny wall.

In the lorica of *Trachelomonas teres* var. *glabra*, *T. Swirenkoi*, MANCHURIA.

Observations on the flagellation of the zoospores will be necessary before it can be said whether this is a species of *Sphaerita* or *Pseudosphaerita*.

OLPIDIUM (BRAUN) RABENHORST

Flora Europaea algarum, 3:288. 1868 (sensu recent. Schroeter,

Kryptogamenfl. Schlesien, 3(1):180. 1885)

(Figure 5 D, p. 78; Figure 6, p. 90)

Chytridium, subgen. *Olpidium* Braun, Abhandl. Berlin Akad., 1855:75.
1856.

Cyphidium Magnus, Wissensch. Meeresunters. Abt. Kiel, 2-3:77. 1875.
Olpidiella Lagerheim, Journ. de Botanique, 2:438. 1888.

Thallus soon becoming walled, endobiotic, holocarpic, without rhizoids, not entirely filling the cell of the substratum, forming either a sporangium or a resting spore; sporangium inoperculate, predominantly spherical or ellipsoidal, smooth-walled, usually forming a single discharge tube (sometimes several) of variable length, the tip, at least, extramatrical; zoospores formed within the sporangium, posteriorly uniflagellate, usually with a single globule, discharged through a pore formed upon the deliquescence or rupturing of the tip of the discharge tube; resting spore thick-walled, generally with a large globule, borne like the sporangium, formed in some instances (all?) from a planozygote produced by the fusion of isogamous planogametes, upon germination forming zoospores.

The genus includes forms parasitic primarily in fresh-water algae, flowering plants, spores, moss protonema (Petersen, 1910; Skvortzow, 1927), and aquatic microscopic animals.

Braun's subgenus, raised to generic rank by Rabenhorst, included *Olpidium apiculatum* (*Entophyscitis*), *O. endogenum*, and *O. Saprolegniae* (*Olpidiopsis*). Rabenhorst emphasized the inoperculate sporangium and the presence of a discharge tube as characters common to all the species regardless of their relation to the substratum. Hence *Rhizophydium ampullaceum* even though epibiotic fell within these limits and was included in the genus. Schroeter (1885:180) established *Olpidium* as it is here understood and as it has been maintained by subsequent monographers, that is, as a genus confined to endobiotic holocarpic chytrids without rhizoids and with one, or occasionally several, discharge tubes. His assertion that the zoospore was anteriorly flagellate is incorrect, however, and probably rests on Fisch's observations on *O. Lemnae* (see p. 107). Because of this character in Schroeter's description of the genus Lagerheim (*loc. cit.*)

was led to establish *Olpidiella* for forms with posteriorly uniflagellate zoospores.

Endolpidium Hormisciae de Wildeman (1894) in *Hormiscia zonata* in France differs from species of *Olpidium* only in forming a short discharge tube which does not penetrate the algal wall and in producing hypertrophy of the host wall. The zoospores and resting spores were not observed. (See p. 128.)

Cyphidium was established by Magnus (*loc. cit.*) as a subgenus of *Chytridium* for *Olpidium*-like forms in which the sporangium rests between the wall and the protoplasm of the host. No combinations, however, were made. (See remarks under *O. zygnemica*, p. 87.) Petersen (1910:504, footnote) applied the generic name *Oligostomum* to "Olpidium-shaped marine forms with uniflagellated zoospores and with a limited number of channels for the zoospores (several *Pleotrichelus* forms)." The description is too inadequate and too vague to be tenable, and no species is named which would typify the genus. *Asterocystis* de Wildeman (1893a:21), erected for an *Olpidium*-like parasite in the roots of terrestrial flowering plants, has been discussed by Karling (1937d).

A genus *Gamolpidium* (*G. nitidis*) is mentioned by Constantineanu (1901) as having been established by Vladescu (1892). The genus cannot be discussed here since Vladescu's paper is apparently not available in this country.

Sexuality has been demonstrated to occur in several species of *Olpidium* parasitic in certain flowering plants (Kusano, 1912, 1929), namely, *O. Viciae* and *O. Trifolii*. Cytological evidence for its occurrence in *O. Agrostidis* has also been presented by Miss Sampson (1932). It has not been convincingly described in any of the purely aquatic species save for the observations of Fisch (1884a) on *Reessia* (see under *O. Lemnae*, p. 108). Yet since Fisch's fungus was said to have anteriorly uniflagellate gametes it can hardly be considered an *Olpidium*.

In *Olpidium Viciae*, Kusano observed that the swarmers copulated in pairs, the zygote then infecting the host and producing within it a resting spore. Swarmers which did not copulate eventually penetrated the host, where each formed a sporangium. A more critical investigation by Kusano of sexuality as it exists in *O. Trifolii* seems to indicate that sister gametes from the same gametangium are usu-

ally incapable of fusing with one another to form a planozygote. He concludes, therefore, that the fungus is dioecious but has a tendency toward monoecism. Another feature of the behavior of the gametes in this species was their aggregation at certain places in the medium. This aggregation was found to have a definite influence in promoting conjugation. Kusano suggests that the groups of nearly stationary gametes, undergoing amoeboid changes of shape, exert an attractive action upon free-swimming ones and thus induce fusion. In both species gametes discharged from recently formed gametangia were not so apt to conjugate as those from somewhat older ones.

In the following analytical key to the species considerable use is made of differences in substrata. In all probability this is not sound, and future work is very likely to reveal that a single species may occur in a variety of substrata. Since the basic morphological plan of an *Olpidium* is very simple there exists little chance for wide variation in this respect. Features such as the length of the discharge tube and the relative position of the fungus and the plasma of the substratum impressed the earlier investigators, but recent work has shown these to be of little taxonomic value.

KEY TO THE SPECIES OF OLPIDIUM

In algae or in plant spores

In Chlorophyceae; sporangium variable in shape; zoospores formed in the sporangium

Sporangium ellipsoidal, spherical, subspherical, pyriform, or ovoid

Sporangium subspherical or broadly ellipsoidal, its long axis parallel with that of the algal cell; discharge tube arising from the middle of the sporangium, thus appearing lateral, with a pronounced endobiotic swelling; in *Conjugatae* *O. endogenum*, p. 86

Sporangium spherical, ellipsoidal, ovoid, or pyriform, endobiotic part of the apical discharge tube isodiametric; in various green algae

Sporangium spherical, ellipsoidal, or ovoid, resting spore smooth-walled

Sporangium spherical, discharge tube not projecting beyond outer surface of the algal wall; in *Zygnema*

O. zygnemicola, p. 87

- Sporangium spherical, ellipsoidal, ovoid, or occasionally somewhat pyriform, discharge tube projecting more or less beyond wall
- Discharge tube strongly constricted when passing through host wall, expanded locally on outer surface and extending extramatrically; in zygospores of *Spirogyra* *O. rostriferum*, p. 88
- Discharge tube isodiametric, extending for varying distances beyond algal wall
- In vegetative cells of various green algae
O. entophytum, p. 88
- In oospores of *Sphaeroplea* *O. Sphaeropleae*, p. 89
- Sporangium pyriform, with a short sessile discharge tube, resting spore spiny; in *Hyalotheca* ... *O. Hyalothecae*, p. 90
- Sporangium somewhat tubular and saclike, constricted in mid-region *O. saccatum*, p. 91
- In Euglenophyceae; sporangium spherical; zoospores formed in an extruded vesicle as well as in the sporangium
O. Euglenae, p. 92
- In diatoms; sporangium spherical, $3.4\text{--}5.5 \mu$ in diameter, opening by a pore; in *Hantzschia* *O. Hantzschiae*, p. 92
- In plant spores
- In pollen grains; sporangium spherical or ovoid; discharge tube short or long
- Sporangium spherical, generally with a short broad discharge tube; zoospores spherical, $4\text{--}5 \mu$ in diameter; penetration tube often persistent on the smooth-walled resting spore *O. pendulum*, p. 93
- Sporangium spherical or ovoid, discharge tube narrow, often prolonged extramatrically; penetration tube not persistent on the spherical or ellipsoidal resting spore
O. luxurians, p. 93
- In rust spores; sporangium spherical or somewhat angular; discharge tube short or only a papilla *O. Uredinis*, p. 94
- [In moss protonema *O. protonemae*¹]
- In animal substrata
- In eggs of rotifers; sporangium spherical, ovoid, ellipsoidal, or irregularly saclike; resting spore lying loosely in a spherical structure; zoospores with a single globule *O. gregarium*, p. 94

¹ Not considered in the present work.

In zoocysts of *Vampyrella*

- Sporangium spherical or broadly ovoid; zoospore without a large refractive globule *O. Vampyrellae*, p. 95
- Sporangium ovoid, somewhat irregular, or, if several in a cell, somewhat tubular; zoospore with a minute eccentric globule *O. Pseudosporearum*, p. 96
- In adult nematodes *O. Nematodeae*, p. 96

OLPIDIUM ENDOGENUM (Braun) Schroeter

Kryptogamenfl. Schlesien, 3 (1):180. 1885

(Figure 5 D, p. 78)

Chytridium endogenum Braun, pro parte, Monatsber. Berlin Akad., 1855:384; Abhandl. Berlin Akad., 1855:60, pl. 5, fig. 21. 1856 (not the forms in *Vaucheria* and *Spirogyra*); Monatsber. Berlin Akad., 1856:588.

Chytridium intestinum Braun, Monatsber. Berlin Akad., 1856:589. Non *C. intestinum* Schenk.

Olpidium intestinum (Braun) Rabenhorst, Flora Europaea algarum, 3: 283. 1868.

Olpidiella endogena (Braun) Lagerheim, Journ. de Botanique, 2:438. 1888.

Sporangium strongly subspherical or broadly ellipsoidal, occasionally spherical, up to 25μ in diameter, its longer axis parallel with that of the alga, wall smooth, slightly thickened, colorless, discharge tube long, 5μ in diameter, arising from the middle of the sporangium, narrowly cylindrical, with a pronounced swelling (6.6μ in diameter) where it meets the inner face of the algal wall, extending for a variable distance extramatrically and terminating in a funnel-like apex; zoospores spherical, 3μ in diameter, with a colorless globule; resting spore spherical, ellipsoidal, or somewhat pyriform, 15μ in diameter, wall smooth, colorless, of two layers, the outer thicker than the inner, contents with a large oil globule, germination not observed.

Parasitic in desmids, *Closterium*, *Pleurotaenium*, *Cosmarium*, *Penium*, *Euastrum*, *Tetmemorus*, *Micrasterias*, etc., Braun (*loc. cit.*), de Bary, Pringsheim (in Braun, 1855:384), Schroeter (1885:180), Cejp (1933a:2, pl. 1, figs. 1-3), Schulz (1922:147, figs. 85b, 86-90; 1923:fig. 3), GERMANY; *Closterium Lunula*, Archer (1860:215, pl. 11, fig. 5), ENGLAND; *Spirogyra majuscula*, Loscos (in Rabenhorst,

1868:283), SPAIN; *Closterium Lunula*, *Closterium sp.*, Sorokin (1874b:4, pl. 1, figs. 1-5; 1883:31, fig. 35), RUSSIA; *Closterium sp.*, Dangeard (1886a:285), desmids, de Brébisson (1856:150), FRANCE; *Cosmarium pachydermum*, Skvortzow (1925:429), MANCHURIA.

Sorokin (1876:63, pl. 3, fig. 1) has placed in this species a fungus with an ellipsoidal sporangium bearing a cylindrical isodiametric curved discharge tube. It occurred in great numbers in eelworms, where it was the first of a series of parasites causing an epidemic in his cultures. The sporangia were closely packed in linear series. As Fischer (1892:24) has suggested, this may in reality be a species of *Myzocytium* or, as is less likely, of *Catenaria*.

Gwynne-Vaughan and Barnes (1937:fig. 11) and Sparrow (1936a: 427, pl. 14, fig. 1) have figured a fungus on filamentous Conjugatae in England which has ellipsoidal sporangia, as does the present species, but which differs from it in having a short stout discharge tube only slightly inflated basally. Future studies of *Olpidium endogenum* may allow the inclusion of this variety.

It is presumed that the measurement (25μ) given by Braun and later authors refers to the longer axis of the sporangium. Resting spores have been found in abundance by Schulz (1922) and Cejp (1933a).

OLPIDIUM ZYGNEMICOLA Magnus

Verhandl. Bot. Vereins Prov. Brandenburg, 26:79. 1885

Sporangium formed between the wall and the contents of the alga, resting directly on the latter, spherical, colorless, smooth-walled, with a discharge tube which does not project beyond the outer wall of the alga; zoospores uniflagellate; resting spore within the contents of the alga, spherical, with a faintly mottled thick smooth wall and a large oil globule, germination not observed.

In *Zygnema sp.*, GERMANY.

The position of the sporangium between the wall and the protoplasm of the alga is by itself of little significance as a character maintaining this species distinct from *Olpidium entophytum*. All gradations in position are often found in an algal cell heavily infected with a species of *Olpidium*.

OLPIDIUM ROSTRIFERUM Tokunaga

Trans. Sapporo Nat. Hist. Soc., 13:80, pl. 5, fig. 11. 1933

Sporangia spherical to ovoid, 14.4–25.2 μ in diameter, singly or from two to five in a zygospore of the host, wall smooth, discharge tube single, up to 70 μ in length, 3–4.2 μ in diameter, strongly constricted when passing through the wall of the zygote and expanded locally (up to 6 μ) on its outer surface, extending for a variable distance outside the gametangium wall; zoospores spherical, about 3.6 μ in diameter, with a single flagellum; resting spore spherical or ellipsoidal, 16.8–24 μ in diameter, from one to three in a zygote, with a smooth golden-yellow wall 1.6 μ thick, contents with a large central globule, germination not observed. (Modified from Tokunaga.)

In zygospores of *Spirogyra Jurgensii*, JAPAN.

OLPIDIUM ENTOPHYTUM (Braun) Rabenhorst

Flora Europaea algarum, 3:283. 1868

(Figure 6 A, p. 90)

Chytridium entophytum Braun, Monatsber. Berlin Akad., 1856:589.

Sporangium spherical; ellipsoidal, ovoid, or somewhat pyriform, 5.7–27.7 μ in diameter, wall thin, smooth, colorless, discharge tube (rarely two) isodiametric throughout, variable in length, up to 14.8 μ long by 3–5.7 μ in diameter; zoospores spherical, 3–5 μ in diameter, with a colorless globule and a long flagellum, forming a temporary, motionless mass at the orifice of the discharge tube; resting spore spherical or ellipsoidal and 11–22.5 μ broad by 18.5–29.6 μ long, wall smooth, thick, colorless, contents dense, germination not observed.

In *Vaucheria globifera* (*salina* ?), de Bary (in Braun, loc. cit.), *Spirogyra*, *Vaucheria*, Kloss (in Braun, loc. cit.), *V. geminata*, *V. sessilis*, Schenk (1858a:237), *Cladophora glomerata*, *Vaucheria*, Schroeter (1885:181), GERMANY; *Vaucheria*, Dangeard (1886a:286, pl. 14, fig. 11), *Cladophora* sp., de Wildeman (1895c:215), FRANCE; *Desmidium Swartzii*, de Wildeman (1893b:49, pl. 7, fig. 4), BELGIUM; *Vaucheria* sp., Constantineanu (1901:370), RUMANIA; *Spirogyra* sp., Skvortzow (1925:428), MANCHURIA; *Spirogyra communis*, *Aegagropila Sauteri*, Tokunaga (1933b:79, pl. 5, figs. 1–3), JAPAN; *Spirogyra* sp., Sparrow (1933c:515), UNITED STATES; *Cladophora* sp., Sparrow (1936a:427, pl. 14, fig. 6), ENGLAND.

All forms with a spherical, ellipsoidal, ovoid, or somewhat pyriform sporangium and an isodiametric discharge tube of variable length which inhabit green algae are included in this species. Cross-inoculation experiments may in the future show the species as now understood to be a collective one.

The fungus on *Aegagropila* reported by Tokunaga (1933b:79), tentatively placed here, forms sporangia ranging from 19.2–62.4 μ in diameter; the discharge tube is broad, attaining a diameter of 9.6 μ .

OLPIDIUM ENTOPHYTUM (?) var. INTERMEDIUM Constantineanu,
Revue Gén. Bot., 13:371, fig. 75. 1901

Sporangium either spherical and 20–30 μ in diameter or elongate and 30–33 μ in diameter, wall thin, smooth, colorless, with a strongly projecting somewhat irregular or undulate discharge tube 108–114 μ long by 6–8 μ in diameter; zoospores and resting spore not observed.

In rotifer eggs, RUMANIA.

If the zoospores of this fungus are found to resemble those of *Olpidium gregarium* it is probably a tenable variety of that species. As was suggested by Constantineanu, it also resembles *O. macrosporum* Nowak. and may be referable to it. That only a single sporangium was formed in Nowakowski's species, whereas from five to twenty were present in var. *intermedium*, is not considered significant.

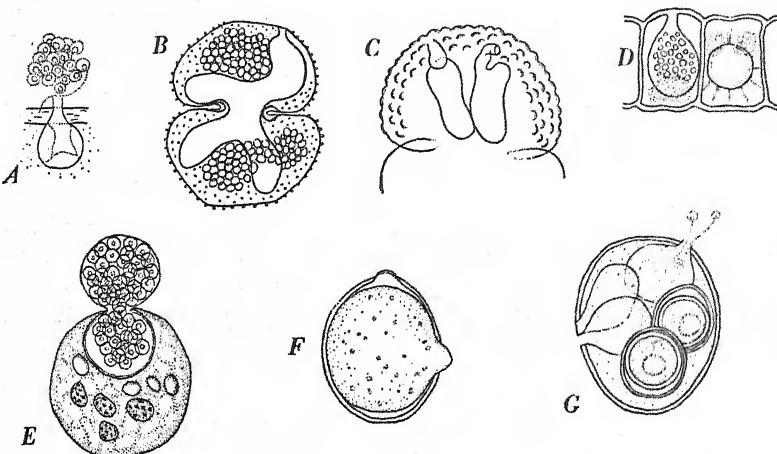
OLPIDIUM SPHAEROPLAE Tokunaga

Trans. Sapporo Nat. Hist. Soc., 13:81, pl. 5, figs. 9–10. 1933

Sporangia spherical, mostly solitary in the oöspores of the host, which they fill at maturity, 12–24 μ in diameter, with a single short cylindrical discharge tube; zoospores ellipsoidal to ovoidal, about 4.8 \times 2.4 μ , uniflagellate; one resting spore, very rarely two, in the oöspores of the host, spherical, 11.4–12.6 μ (mostly 12 μ) in diameter, with a smooth slightly golden wall 1 μ thick, contents with a large globule, germination not observed.

In oöspores of *Sphaeroplea annulina*, JAPAN.

The sporangia of this species resemble those of *Rozella* in their tendency to fill the oöspore of the host.

FIG. 6. *Olpidium*

A. *Olpidium entophytum* (Braun) Rabenhorst, ($\times 450$), discharged sporangium in *Cladophora*. B. *Olpidium utriculiforme* Scherffel ($\times 370$), empty sporangium in *Cosmarium*. C. *Olpidium saccatum* Sorokin ($\times 250$), empty sporangia in semicell of *Cosmarium*. D. *Olpidium Hyalothecae* Scherffel ($\times 370$), zoosporangium and spiny resting spore in cells of *Hyalotheca*. E. *Olpidium Euglena* Dangeard, discharging sporangium in *Euglena* cyst. F-G. *Olpidium gregarium* (Nowak.) Schroeter ($\times 350$) in rotifer eggs: F, single sporangium with discharge papilla protruding through wall of egg case; G, empty and discharging sporangia and resting spores.

(A, F-G, Sparrow, 1936a; B-C, Scherffel, 1926a; D, after Scherffel, 1926a; E, Dangeard, 1894-95b)

OLPIDIUM HYALOTHECAE Scherffel

Arch. Protistenk., 54:200, pl. 9, figs. 62-63. 1926

(Figure 6 D)

Sporangia pyriform, with a smooth colorless thin wall, one or two, rarely three, occupying the greater part of the host cell, 15-19 μ in diameter and 28 μ long, forming a short discharge tube which grows to the outer surface of the host cell; zoospores spherical, with a single basal oil droplet and a long delicate posterior flagellum, motion hopping; resting spore spherical, 8-12 μ in diameter with a thickened wall the outer surface of which bears a few straight faintly refractive rodlike spines, germination not observed.

On *Hyalotheca dissiliens*, HUNGARY.

OLPIDIUM SACCATUM Sorokin

Arch. Bot. Nord France, 2:30, fig. 33 a-d. 1883 (separate)¹

(Figure 6 C)

Sporangium swollen and short sausage- or saclike, smooth, thin-walled, constricted in the mid-region, with a somewhat conical end resting against the inner surface of the host cell and by means of a circular pore opening at the level of the outer host wall to the outside at maturity, or, if the sporangium body does not directly make contact with the wall, forming a short, or rarely elongate and bent, sharply defined cylindrical discharge tube the open apex of which is just level with the outer surface of the host wall but never extends beyond it; zoospores minute, typically chytridiaceous with the characteristic oil droplet; resting spore apparently asexually formed by contraction of the protoplasm of the thallus, nearly spherical or somewhat pyriform, colorless, 11-16 μ in diameter, mostly 14-15 μ high by 16 μ in diameter, wall about 2 μ thick, the outer layer appearing dark and of double contour, the inner faintly refractive, contents with a densely crowded group of strongly refractive (oil?) coarse granules or with a single large fat droplet, the spore lying in the spherical widened end of the thin-walled tube, from which it is separated by a cross wall, germination not known.

In desmids, Sorokin (*loc. cit.*), ASIATIC RUSSIA; *Cosmarium* sp., de Wildeman (1893b:50, pl. 6, figs. 17-25), BELGIUM; *Staurastrum* sp., *Cosmarium* sp. (coll. Massart), de Wildeman (1896b:46, pl. 3, figs. 29-32), NORWAY, FRANCE; *Cosmarium Botrytis*, *Cosmarium* sp., Scherffel (1926a:210, pl. 10, figs. 80-83), HUNGARY.

Fischer and others after him consider the distinctive constriction characteristic of this species to be brought about by conditions imposed upon the sporangium by the shape of the host cell. Scherffel, however, has found such constricted sporangia lying wholly within one semicell of the desmid. Furthermore, the posteriorly uniflagellate zoospores observed by Scherffel throw doubt on the possibility that his fungus could have been a depauperate species of the laterally biflagellate genus *Myzocytium* (see p. 648) rather than the present species *Olpidium saccatum*, which it resembles, moreover, in all other respects.

¹ See also Sorokin, *Revue Mycologique*, 11:136, pl. 79, figs. 86-89. 1889.

OLPIDIUM EUGLENAE Dangeard

Le Botaniste, 4:248, fig. 10 A-F. 1894-95

(Figure 6 E, p. 90)

Sporangium spherical, with a slightly thickened colorless smooth wall, lying eccentrically and loosely in the host cell; zoospores spherical, with a small centric yellow-orange globule and a long posterior flagellum, formed in the sporangium as well as in an extramatrical vesicle which is extruded through a wide sessile pore to the outside of the host cell, escaping upon the dissolution of the vesicle, movement hopping; resting spore not observed.

Parasitic in *Euglena sp.*, FRANCE (rare).

The species differs from other members of the genus in the method of formation of the zoospores. Further observations may indicate that it should be segregated from *Olpidium*. At maturity the sporangium opens by a sessile pore to the outside of the host and there forms a sac equal to or exceeding the endobiotic part in size. The protoplasm of both parts is then quickly divided into zoospores. In this unusual instance the endobiotic part functions both as a prosporangium and a sporangium. From Dangeard's Figure B it is also apparent that sometimes at least the globules of the spores are already organized before extrusion of the vesicle.

OLPIDIUM HANTZSCHIAE Skvortzow

Arch. Protistenk., 51:430, text figs. 3-4. 1925

Sporangia spherical, from nine to twenty-seven in the abnormally swollen host cell, $3.4-5.5 \mu$ in diameter, without projecting discharge papilla or tube, opening by a pore; zoospores at first spherical, then egg-shaped, with a colorless oil droplet and a long flagellum, 3.4μ long by $1.5-1.7 \mu$ in diameter; resting spore spherical, $5-6 \mu$ in diameter, with dense plasma and a smooth wall, germination not observed.

In *Hantzschia Amphioxys*, MANCHURIA.

In its small size, lack of a discharge tube, and general habit the organism strongly resembles a flagellate, particularly *Aphelidium*.

OLPIDIUM PENDULUM Zopf

A. Schenk, Handbuch d. Bot. . . . , 4:555, fig. 66 (1-5). 1890

Sporangia spherical, with a slightly thickened smooth wall, up to twelve in a host cell, up to $30\ \mu$ in diameter and with a short broad discharge tube when occurring singly, smaller and with a long narrow discharge tube when there are several in a cell; zoospores spherical, $4-5\ \mu$ in diameter, with a small colorless basal globule and a long flagellum, movement lively; resting spore spherical, with a smooth thick wall and a large globule, infection tube often persistent, appearing as an appendage, germination not observed.

In pine pollen, Zopf (*loc. cit.*), GERMANY; (?) pollen, Voronichin (1920:9), RUSSIA; pollen of *Pinus ponderosa*, Graff (1928:158), UNITED STATES.

Differs from *Olpidium luxurians* in having larger zoospores and a resting spore which completely fills its container.

OLPIDIUM LUXURIANS (Tomaschek) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):29. 1892

Chytridium luxurians Tomaschek, Sitzungsber. Acad. Wiss. Wien (Math.-Nat. Cl.), 78:204, figs. 1, 3-4, 6-11. (1878) 1879.

Diplochytrium sp., *ibid.*, p. 198.

Chytridium pollinis-typae forma *latifoliae*, *ibid.*, p. 203.

Olpidium Diplochytrium (Tomaschek) Schroeter, Kryptogamenfl. Schlesien, 3 (1):181. 1885.

Olpidiella Diplochytrium Lagerheim, Journ. de Botanique, 2:439. 1888.

Sporangia spherical or ovoid, up to thirty in a pollen grain, of different sizes, up to $40\ \mu$ in diameter, wall smooth, colorless, discharge tube narrow, often somewhat curved and prolonged outside the substratum; zoospores somewhat elongate, with rounded apex and narrow end, $2\ \mu$ in diameter, movement even or undulate, swimming; resting spore spherical or somewhat ellipsoidal, $20\ \mu$ in diameter, with a thin smooth wall and a large oil globule, resting in a larger, thick-walled, structure $24\ \mu$ in diameter, upon germination forming zoospores.

In pollen of *Pinus*, *Taxus*, *Lillium*, *Typha*, *Cannabis*, etc., Tomaschek (*loc. cit.*), AUSTRIA; *Pinus*, Schroeter (1885:181), pollen, Minden (1915:240), GERMANY; *Picea excelsa* pollen, Rostrup (1896:

126), Petersen (1910:554, fig. 25a), DENMARK; *Pinus koraiensis*, Skvortzow (1927:206), MANCHURIA.

The resting spores usually germinated after the disintegration of the pollen grain.

OLPIDIUM UREDINIS (Lagerheim) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):30. 1892

Olpidiella Uredinis Lagerheim, Journ. de Botanique, 2:438, pl. 10, figs. 1-15. 1888.

Sporangia spherical when occurring singly, or angular and smaller when there is more than one in the host cell, 26μ in diameter, with a delicate hyaline or subhyaline smooth wall, forming a short discharge tube which pierces the wall, or only a papilla; zoospores ellipsoidal, posteriorly uniflagellate, with a single globule, $3-4 \mu$ in diameter; resting spore endobiotic, globose, with a thick colorless smooth wall, 16μ in diameter, contents colorless, with a large oil globule.

In uredospores of *Puccinia Airae*, *P. Violae*, and *P. Rhamni*, but not capable of infecting uredospores of certain other rusts, GERMANY.

OLPIDIUM GREGARIUM (Nowak.) Schroeter

Kryptogamenfl. Schlesien, 3(1):182. 1885

(Figure 6 F-G, p. 90)

Chytridium gregarium Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2: 77, pl. 4, fig. 2. 1876.

Sporangia spherical, ovoid, ellipsoidal, or irregularly saclike, the spherical ones $30-70 \mu$ in diameter, the ovoid and ellipsoidal ones $18-35 \mu$ long by $17-32 \mu$ in diameter, with a single short broad papilla $7-10 \mu$ in diameter which protrudes through the wall of the egg, wall thin or slightly thickened, smooth, colorless; zoospores spherical, $2.5-4 \mu$ in diameter, with a single eccentric refractive globule and a long flagellum, emerging through a pore formed at the tip of a nearly sessile or slightly protruding discharge tube and either forming a temporary compact mass surrounded by a quickly evanescent slime film or swimming directly away, movement swimming and amoeboid; resting spore sometimes lying loosely in a spherical containing structure, spherical, brownish, thick-walled, the wall up to 6μ thick,

smooth or with faint striations, 15–20 μ in diameter, containing a large globule, germination not observed.

Parasitic on rotifer eggs, Nowakowski (*loc. cit.*), E. J. Butler (1907:136, pl. 8, figs. 13–18), (coll. [?] Hieronymus) Schroeter (1885:182), GERMANY; eggs of *Brachionus sp.*, adults of *Euchlanis sp.*, Tokunaga (1933b:79, pl. 5, figs. 4–7), JAPAN; Sparrow (1936a: 427, pl. 14, figs. 2–4), ENGLAND; Petersen (1910:554), Sparrow (*loc. cit.*), DENMARK.

The shape of the sporangium, as in other endobiotic chytrids, undergoes considerable modification when more than one fungus is present within the limited confines of the substratum. Here, the sporangia often tend to be smaller and to lose their regular ellipsoidal or spherical shape and become irregular and saclike.

Zoospores of an undescribed parasite of rotifer eggs "near *O. gregarium*" are described by Scherffel (1925a:66, pl. 5, fig. 222). They differ from those of the present species in containing several globules rather than one. Both Butler and Sparrow have noted that the resting spores sometimes lie loosely in a surrounding membrane. The former has suggested that this has come about from the fact that the fungus gained entrance after segmentation of the animal embryo had occurred. Since some of the sporangia in Butler's material were similarly placed, this seems plausible. It is also possible that the spores arise by contraction and subsequent walling of their protoplasm, as in some species of *Pythium*.

The protoplasm of the eggs attacked by Nowakowski's fungus was pinkish and the thallus of the chytrid was similarly colored. The zoospores, however, appeared to be colorless. From the remarks of Fischer (1892:31), it is probable that he observed the fungus, but the host is not given.

OLPIDIUM VAMPYRELLAE Scherffel

Arch. Protistenk., 54:168, pl. 9, figs. 2–5. 1926

Sporangium spherical or broadly ovoid, colorless, 10–12 μ in diameter or 12–13 \times 14–15 μ , with a short papilla-like refractive discharge tube 3–4 μ long by 2 μ wide which bores through the host wall; contents of the sporangium during maturation bearing small contractile vacuoles and exhibiting a slight amoeboid movement; zoospores moving in the sporangium before escape, discharged with

the watery content of the tube upon the dissolution of its tip, each spore resting a moment at the tip of the sporangium before swimming away, body somewhat ovoid, $3 \times 2 \mu$, with dense shining contents nearly free of granules and without an oil drop, with a single posterior flagellum; resting spore not observed.

In zoocysts of *Vampyrella*, HUNGARY.

Although forming contractile vacuoles and lacking an oil globule in the zoospore the organism is believed by Scherffel to be a species of *Olpidium* rather than a monad.

OLPIDIUM PSEUDOSPOREARUM Scherffel

Arch. Protistenk., 54:170, pl. 9, figs. 6-7. 1926

Sporangia ovoid or somewhat irregular, becoming rather tubular if several occur in a cell, usually 12μ long by 9μ in diameter, varying in size according to the number occupying a single zoocyst, wall thin, colorless, smooth; plasma whitish, gleaming, with numerous minute oil droplets; discharge tube short, papilla-like, penetrating the host wall; zoospores very numerous, small, spherical, with an eccentric minute (1μ) oil droplet and a very long posterior flagellum, movement hopping, gliding; resting spore not observed.

In zoocysts of *Pseudosporopsis Bacillariacearum* (?) and *Pseudospora parasitica* (?), HUNGARY.

Zopf (1888:351) also mentions an *Olpidium* in the zoocyst of *Pseudospora*. This fungus, however, formed a long discharge tube, thus differing from the present species. *O. Pseudosporrearum* differs from *O. Vampyrellae* in that the zoospore possesses a globule. Furthermore, the sporangium has a less prominent discharge tube. Scherffel has not distinguished this species from *O. Diffugiae*.

OLPIDIUM NEMATODEAE Skvortzow

Arch. Protistenk., 57: 204, fig. 1. 1927

Sporangia occurring singly or in linear series, spherical, $15-35 \mu$ in diameter, with a smooth thin wall, discharge tube narrowly cylindrical, $100-180 \mu$ long by 7μ in diameter, extending beyond the host wall; zoospores uniflagellate; resting spore $25-32 \mu$ in diameter, wall smooth, 5μ thick, of two layers.

In nematodes, Skvortzow (*loc. cit.*), MANCHURIA; cysts of *Heterodera Schachtii*, Rozsypal (1934:413, pl. 2, figs. 72-79), GERMANY.

IMPERFECTLY KNOWN SPECIES OF OLPIDIUM

In Marine Algae

? OLPIDIUM AGGREGATUM Dangeard

Le Botaniste, 2:237, pl. 16, figs. 25-26. 1890-91

Sporangium ovoid or ellipsoidal, its long axis parallel with that of the host cell, with a long discharge tube arising at right angles from the mid-region, its tip just penetrating the host wall or extending slightly beyond it, wall stout, smooth, colorless; zoospores spherical, with a colorless refractive globule, escape and flagellation not observed; resting spore not observed.

Occurring in linear aggregates in a marine species of *Cladophora*, FRANCE.

To judge from the shape of the sporangia of this species, as well as from the fact that they occurred in linear aggregates in the alga, it is very probable that Dangeard was dealing with *Siroolidium*. Since the flagellation of the zoospores was not observed, this cannot now be said with certainty.

Tokunaga (1933b:79, pl. 5, fig. 8) has recently reported this species from Japan, where it was found in a marine *Cladophora*. The sporangia, which were described as narrowly ellipsoidal to cylindrical, sometimes irregular, and $26.4-90 \times 12-27.6 \mu$, were said to discharge narrowly ellipsoidal uniflagellate zoospores. The zoosporangia figured closely resemble in shape, location within the host, and vacuolization those formed by *Siroolidium Bryopsidis*.

? OLPIDIUM ENTOSPHAERICUM (Cohn) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):27. 1892

Chytridium (?) *entosphaericum* Cohn, Hedwigia, 4:170. 1865; Schultze, Archiv. micro. Anat., 3:43, pl. 2, figs. 5, 5a. 1867.

Sporangium spherical, colorless, 16μ in diameter, single in cells of the host, filling or partly filling the host cell.

In *Bangia fuscopurpurea* and *Hormidium penicilliformis*, GERMANY.

? OLPIDIUM LAGUNCULA H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):
466, fig. I, 1-2

Sporangium variable in shape, more or less spherical or irregularly bottle-shaped, $12-45 \mu$ long by $13-33 \mu$ in diameter, with a thin smooth wall, discharge tube $10-55 \mu$ in length; other characters unknown.

In *Dumontia filiformis*, DENMARK.

? OLPIDIUM LAUDERIAE Gran

Nyt Mag. Naturvid., 38 (2):123, pl. 9, figs. 8-9. 1900

Sporangium broadly ovoid, slightly irregular and bent, discharge tube broad and short, penetrating the wall of the host, the border of the orifice somewhat recurved and flangelike.

On *Lauderia borealis*, NORWAY (fixed material).

Said to be a species of *Eurychasma* by Petersen (1905: 469), who calls it *E. Lauderiae* (Gran) H. E. Petersen, but considered a species of *Ectrogella* by Scherffel (1925a: 3), who applies to it the binomial *Ectrogella Lauderiae* (Gran) Scherffel. Until the zoospores are observed it is impossible to say which of the three available combinations should be used.

? OLPIDIUM PLUMULAE (Cohn) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):27. 1892

Chytridium Plumulae Cohn, Hedwigia, 4:169. 1865; Schultze, Archiv. micro. Anat., 3:59, pl. 1, figs. 21-23. 1867.

Phlyctidium Plumulae (Cohn) Rabenhorst, Flora Europaea algarum, 3:279. 1868.

Sporangium inducing a rudimentary branchlike outgrowth of the host wall, ovoid or subglobose, lying between the wall and the host contents, without rhizoids, 15μ in diameter, reddish or dark red; zoospores very numerous, discharged through an irregular lateral opening.

In *Antithamnion Plumulae*, Cohn (*loc. cit.*), GERMANY; *Calithamnion Plumulae*, Magnus (1875: 77), DENMARK.

The identity of this fungus cannot be determined without further observations on the zoospores. It may be *Eurychasmidium tumefaciens* (Magnus) Sparrow.

Fischer (*loc. cit.*) gives *Chytridium Antithamnii* Cohn and *Cyphidium Plumulae* Magnus as synonyms.

In Fresh-Water Algae

? *OLPIDIUM ALGARUM* Sorokin

Arch. Bot. Nord France, 2:30, fig. 32. 1883 (separate)¹

Olpidium algarum var. *longirostrum* Sorokin, *loc. cit.*

Sporangium narrowly ellipsoidal, wall thin, smooth, colorless, resting with its long axis parallel with that of the algal cell, forming at one end a long, moderately broad, somewhat curving discharge tube with a funnel-like apex, which extends slightly beyond the outer wall of the alga; all other characters unknown.

On "Confervacées" (*Tribonema* ?), ASIATIC RUSSIA.

There is no *Olpidium algarum* of which two varieties, *longirostrum* and *brevirostrum*, have been described, and the former has therefore been taken as the type.

From the illustration given, the alga appears to be a *Tribonema*-like form. The cross wall shown between the parts of the two cells figured has apparently been stimulated to protective-plug formation, probably by another fungus. The sporangia have been calculated from the figures to be about 6 μ high by 12 μ wide, the tube about 12 μ long.

The species is not considered distinct from *Olpidium entophytum* by Fischer (1892: 25) and Minden (1915: 243).

De Wildeman (1893b: 49, pl. 7, fig. 4), using the name *Olpidium algarum* Sorokin describes a form in *Desmidium Swartzii* from Belgium which resembles Sorokin's var. *brevirostrum* in the shape of its sporangium, but which possesses a somewhat longer discharge tube. He suggests that the length of the tube depends on the size of the host cell, and, while he would conserve the name *O. algarum*, his form would be intermediate between the two varieties.

¹ See also Sorokin, *Revue Mycologique*, 11:84, pl. 80, fig. 96. 1889.

? *OLPIDIUM ALGARUM* var. *BREVIROSTRUM* Sorokin, Arch. Bot. Nord France, 2:30, fig. 32 bis. 1883 (separate)¹

Sporangium spherical or broadly ellipsoidal, variously oriented in the algal cell, wall thin, smooth, colorless, discharge tube arising from one of the ends, short, narrow, isodiametric, protruding slightly beyond the outer wall of the alga; zoospores with a swollen, somewhat reniform apex and a colorless basal globule, flagellum fairly long; resting spore not observed.

In *Sphaerozosma vertebratum*, EUROPEAN RUSSIA, ASIATIC RUSSIA.

As suggested by Fischer (1892:25) and Minden (1915:243) the species is only doubtfully distinct from *Olpidium entophytum*.

The sporangia have been calculated to be $4 \times 6-9 \mu$; the zoospores, 1μ in diameter, and the discharge tube, about 2μ long.

? *OLPIDIUM GILLII* de Wildeman

, Ann. Soc. Belge Micro. (Mém.), 20:42. 1896

Sporangia ellipsoidal, from one to three in a host cell, variable in size, wall smooth, colorless, giving a cellulose reaction, discharge tube long; zoospores numerous, structure unknown; other characters unknown.

On *Pleurosigma attenuatum*, *Cocconema lanceolatum*, *Nitzschia* sp., *N. sigmoidea*, coll. Gill, ENGLAND.

The species, of uncertain generic affinities, is based on one of two parasites in diatoms described by Gill (1893:1, figs. 1-8). Scherffel (1925a:2) thinks it possible that Gill's fungi as well as those of van Heurck (1899) are species of *Olpidium*, but owing to the cellulose reaction of the wall this is considered doubtful. He seems to intimate also an affinity with *Olpidiopsis*. Gill states that only *Pleurosigma* was parasitized in his culture dishes during one period of observation. The diatoms in these cultures were collected during November and December. Another collection during March (of a later year) showed only a *Bacillaria* (or small straight *Nitzschia*) to be infected. In both instances other diatoms were in the cultures but were not attacked. At least two different fungi were probably involved, one of which (Gill, *op. cit.*, fig. 9) is said by Scherffel to be in all likelihood a species of *Ectrogella* or *Aphanomyopsis*.

¹ See also Sorokin, *Revue Mycologique*, 11:85, pl. 80, fig. 101. 1889.

? OLPIDIUM IMMERSUM Sorokin

Arch. Bot. Nord France, 2:31, fig. 34. 1883 (separate)¹

Sporangium broadly and somewhat irregularly saclike, slightly constricted in the region of the isthmus of the semicells of the host, wall thin, smooth, colorless, discharge tube narrow, markedly swollen where it meets the inner wall of the host, projecting for a variable distance extramatrically; other characters not observed.

In various desmids, *Staurastrum*, Sorokin (*loc. cit.*), ASIATIC RUSSIA; *Cosmarium*, *Staurastrum*, de Wildeman (1893b:51, pl. 7, figs. 12-15, 17), BELGIUM; *Cosmarium sp.*, de Wildeman (1895a: 65, pl. 2, figs. 1-6), SWITZERLAND; desmid (coll. Massart), de Wildeman (1896b:45, pl. 3, figs. 27-28), NORWAY.

Scherffel (1926a:218) believes this to be the same organism figured by Reinsch (1878:pl. 17, figs. 11-12). The fungus in *Cosmarium* from Denmark, called by Petersen (1910:538, fig. XVIId) *Myxocystium irregulare*, also resembles *Olpidium immersum*. It is unfortunate that, in spite of the relatively numerous collections of this fungus, no observations on the zoospores have been made. Only after this has been done can its true relationships be decided.

? OLPIDIUM (?) MESOCARPI de Wildeman

Ann. Soc. Belge Micro. (Mém.), 20:45, pl. 1, figs. 13-16. 1896

Sporangium smooth, ellipsoidal, more or less elongate, about 10 μ in diameter by 20-28 μ long, single, sometimes two sporangia in one cell of the host and then occupying all the width of the filament, discharge tube lacking, the papilla which perforates the algal wall forming upon its deliquescence a circular opening in the wall for the escape of the zoospores; zoospores and resting spore unknown.

In *Mesocarpus sp.*, BELGIUM.

Differing from most species of the genus in sometimes filling the host cell and in not forming a discharge tube. In these respects it resembles a *Rozella*.

¹ See also Sorokin, *Revue Mycologique*, 11:136, pl. 79, figs. 91-92. 1889.

? OLPIDIUM MOUGEOTIA Skvortzow

Arch. Protistenk., 51:430, fig. 2. 1925

Sporangium spherical, $11\text{--}14.8 \mu$ in diameter, with a short straight isodiametric discharge tube $5.7\text{--}6 \mu$ long, the tip of which does not project beyond the outer surface of the algal wall; other characters unknown.

On *Mougeotia scalaris*, MANCHURIA.

? OLPIDIUM PUSILLUM (Sorokin) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:16. 1896

Chytridium pusillum Sorokin, Arch. Bot. Nord. France, 2:24, fig. 23. 1883 (separate).¹ Non *C. pusillum* Scherffel, Arch. Protistenk., 73:143. 1931.

Sporangium spherical, 4.5μ in diameter, with a very short sessile discharge tube, wall thin, smooth, colorless; other characters unknown.

In cells of *Oedogonium sp.*, EUROPEAN RUSSIA, ASIATIC RUSSIA.

? OLPIDIUM ROSTRATUM de Wildeman

La Notarisia, 10(3):35. 1895; Ann. Soc. Belge Micro. (Mém.), 20:40, fig. 1. 1896

Sporangium narrowly ellipsoidal or somewhat tubular, $28\text{--}40 \mu$ long by 6μ in diameter, the long axis parallel with that of the alga, with rounded ends, one of which bears a slightly bent spinelike prolongation 4.5μ long, wall thin, smooth, colorless, discharge tube narrow, slightly prolonged beyond the algal wall, arising from the middle or end of the sporangium; other characters unknown.

In *Closterium sp.*, coll. Massart, NORWAY.

Observed only in fixed material of the desmid. The peculiar spinelike process may in reality be the axis of a rhizoidal system the remainder of which has been dissolved by the fixing solution. The organism strongly resembles *Mitochytridium*.

¹ See also Sorokin, *Revue Mycologique*, 11:82, pl. 80, figs. 112-113. 1889.

? OLPIDIUM SOROKINEI de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:16. 1896

Olpidiopsis Sorokinei de Wildeman, Ann. Soc. Belge Micro. (Mém.), 14:22, fig. 7. 1890.

Sporangium narrowly tubular or somewhat saccate, its long axis parallel with that of the algal cell, with a short sessile lateral discharge tube, wall thin, smooth; zoospores very small, movement rapid, flagellation not observed; resting spore not observed.

In *Tribonema bombycina*, BELGIUM.

Empty sporangia exactly like those figured by de Wildeman have been found in *Tribonema bombycina* in Michigan. They were accompanied by a resting stage essentially like that in *Olpidiopsis Oedogoniarum* and it is possible that de Wildeman's fungus is really a species of that genus. He separated it from *O. fusiforme* var. *Oedogoniarum* (*O. Oedogoniarum*) chiefly on the basis of difference in host plants.

? OLPIDIUM SPIROGYRAE Skvortzow

Arch. Protistenk., 51:429, text fig. 1. 1925

Sporangium ellipsoidal, with a smooth somewhat stout colorless wall, 33.3-34 μ long by 14.8-15 μ broad, bearing a more or less projecting discharge tube, 7.4-9.2 μ long by 3.7-5 μ broad, which is swollen beneath the host wall, forming a bulblike expansion 3.7 μ wide, and is constricted where it arises from the sporangium; other characters not observed.

In *Spirogyra inflata*, MANCHURIA.

? OLPIDIUM STIGEOCLONII de Wildeman

Mém. Herb. Boissier, 1900 (15):3; Bull. Acad. Roy. Belg. (Sci.), V, 17:297, pls. 1-2. 1931

Sporangia spherical and ellipsoidal when occurring singly, flattened on the face of mutual contact and causing a marked swelling of the host cell when more than one, wall thin, smooth, colorless, discharge tube broad, short or extending for a considerable distance outside the host cell, expanded distally; normal zoospore discharge and typical zoospores apparently not observed; resting spore not observed.

In *Stigeoclonium*, coll. Massart, BELGIUM.

It is probable from the confusing description and explanation of zoospore discharge that this process was observed by de Wildeman neither adequately nor under normal conditions. The spores are said to emerge slowly one by one; they then undergo amoeboid movement, form flagella (more than one?), and detach themselves from the group. According to the account of spore discharge in the explanation of de Wildeman's Plate I the spore loses its flagellum after discharge and moves amoeboidly away. De Wildeman suggests that the sporangia with short tubes are the normal ones, formed at night, and that they liberate normal zoospores. The long-tubed types discharge amoeboid spores during the day.

? OLPIDIUM TUBA Sorokin

Arch. Bot. Nord France, 2:33, fig. 39. 1883 (separate)¹

Sporangium broadly ellipsoidal, its long axis parallel with that of the alga, wall thin, smooth, colorless, discharge tube arising from one end, swollen beneath and on the outer surface of the algal wall, constricted where passing through the wall and terminating in a short narrow isodiametric part; other characters not observed.

In "Confervacees," EUROPEAN RUSSIA, ASIATIC RUSSIA.

? OLPIDIUM UTRICULIFORME Scherffel

Arch. Protistenk., 54:213, pl. 10, figs. 84-87. 1926

(Figure 6 B, p. 90)

Sporangium usually occupying both algal semicells, irregular, tubelike, a simple sac or with a bulging outgrowth or several broad finger-like branches, wall thick, smooth, colorless, forming a single sessile discharge pore; zoospores not observed, contents of sporangium producing uniformly dispersed refractive oil globules 1.5μ in diameter and hence probably forming chytridiaceous spores.

In desmids, *Cosmarium Botrytis*, HUNGARY.

The species resembles *Mitrochytridium ramosum*, but lacks the rhizoids and the several discharge tubes of that genus. Another form (Scherffel, *op. cit.*, pl. 10, fig. 88), on a desmid, was considered

¹ See also Sorokin, *Revue Mycologique*, 11:186, pl. 80, fig. 97. 1889.

by Scherffel to represent a combination of *Olpidium saccatum* and *O. utriculiforme*.

The species appears close to *Olpidium saccatum* Sorokin, as Scherffel indicates.

In Microscopic Animals

? *OLPIDIUM ARCELLAE* Sorokin

Arch. Bot. Nord France, 34, fig. 40. 1883 (separate)¹

Sporangium spherical or subspherical, wall thin, smooth, colorless, with a long, isodiametric, slightly curved or undulate discharge tube which emerges through the pseudopodial opening of the animal shell; other characters not observed.

Saprophytic (?) on the protozoan *Arcella*, EUROPEAN RUSSIA.

? *OLPIDIUM (?) DIFFLUGIAE* Scherffel

Arch. Protistenk., 54:168, pl. 9, fig. 1. 1926

Sporangium broadly pyriform, 23 μ long by 15 μ in diameter, with a thin colorless smooth wall, discharge tube consisting of a broadly conical papilla which does not emerge from the host cell; other features not observed.

In *Diffugia* sp. (Rhizopoda), HUNGARY.

Said to differ from *Olpidium Arcellae* Sorokin and *O. gregarium* in the lack of a well-defined discharge tube. Just how much significance is to be attached to this difference is doubtful, since from the figure given the sporangium appears immature. It seems probable that the tip of the discharge tube eventually becomes extra-matrical.

? *OLPIDIUM LEPTOPHYRDIS* Scherffel

Arch. Protistenk., 54:171, pl. 9, fig. 8. 1926

Sporangium spheroidal, wall thin, smooth, colorless, forming a broad conical, slightly tapering, mostly extra-matrical discharge tube equal to the sporangium in length; other characters unknown.

On zoocyst of *Leptophys vorax*, HUNGARY.

¹ See also Sorokin, *Revue Mycologique*, 11:137, pl. 80, figs. 102-105. 1889.

? OLPIDIUM MACROSPORUM (Nowak.) Schroeter

Kryptogamenfl. Schlesien, 3(1):182. 1885

Chytridium macrosporum Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2:79, pl. 4, figs. 3-4. 1876.

Sporangia occurring singly in the eggs of the host, nearly filling these and hence ovoid, 55μ long by 30μ in diameter; zoospores ellipsoidal, 10μ long by 6μ broad, with finely granular contents and lighter central region, but without a pronounced refractive droplet, number and position of flagella not observed, escaping through a broad tube which exceeds 150μ in length and which pierces the wall of the egg, the lower part of the tube persisting after discharge.

In rotifer (?) eggs, GERMANY.

Differing from *Olpidium gregarium* in occurring singly in the egg, in having a long discharge tube, and in forming large zoospores which lack a refractive droplet. Nowakowski states that the spores are formed in the same manner as in the Saprolegniaceae. From this fact, as well as from the large size of the spores and their want of a refractive globule, it is possible that the fungus is in reality a saprolegnian rather than a chytrid.

? OLPIDIUM ZOOTOCUM (Braun) Sorokin

Arch. Bot. Nord France, 2:33, fig. 38. 1883 (separate)¹

Chytridium zootocum Braun, Monatsber. Berlin Akad., 1856:591.

Sporangium elongate, tubular, curved, discharge tube arising laterally and extending funnel-like beyond the wall of the animal.

In *Anguillula*, coll. Claparede, GERMANY.

Schroeter (1885:182) has placed in this species a parasite of *Anguillula* with a tubular sporangium which remains attached by an attenuated end to the cyst (5μ in diameter) of the infecting zoospore. He questions, justifiably, the identity of his fungus with Braun's. Sorokin's fungus, found in the claw of a dead crustacean in European and Asiatic Russia, has a spherical sporangium and a narrow discharge tube.

The original description is too lacking in essential information to make it possible to refer any fungus to the species.

¹ See also Sorokin, *Revue Mycologique*, 11:136, pl. 79, fig. 90. 1889.

EXCLUDED SPECIES OF OLPIDIUM

* **OLPIDIUM ELLIPTICUM** (Dang.) Saccardo and Traverso

Sylloge fungorum, 20:217. 1911

Minutularia elliptica Dangeard, Le Botaniste, 2:241, pl. 16, figs. 29-31.
1890-91.

Saccardo and Traverso have placed Dangeard's organism in the chytrids, although Dangeard states that it ingests solid particles of food and is a monad.

* **OLPIDIUM INDICUM** Wallich

Turner, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 5, No. 10:164,
pl. 21, fig. 8. 1892

On *Oedogonium sp.* Unquestionably a choanoflagellate.

* **OLPIDIUM LACERANS** de Bruyne

Arch. de Biol., 10:104, pl. 5, figs. 28-31. 1890

Not a fungus. The zoospores contain chlorophyll residue. The figures refer to the monad *Aphelidium lacerans*.

* **OLPIDIUM LEMNAE** (Fisch) Schroeter

Kryptogamenfl. Schlesien, 3 (1):181. 1885

Chytridium Lemnae Fisch, Sitzungsber. Phys.-Med. Soc. Erlangen, 16:43,
pl. 1, figs. 7-9. 1884.

Sporangium spherical, thin-walled, with a thin smooth colorless wall and a long narrow slightly irregular discharge tube; zoospores spherical, with a small colorless globule and an anterior flagellum from two to three times as long as the body, remaining for a short time at the mouth of the discharge tube, motion lively; resting spore spherical, with a double wall, the outer thin and cuticularized, the inner refractive, contents with from one to two large globules and a peripheral bright spot, upon germination producing zoospores.

In cells of *Lemna minor*, *L. polyrrhiza*, Fisch (*loc. cit.*), *L. trisulca* (coll. Hieronymus), Schroeter (1885:181), GERMANY.

If Fisch's observations on the anterior flagellation of the zoospore are presumed to be correct, the organism cannot be a species of *Olpidium*, but, rather, may be related to the Hypochytriaceae.

The genus *Reessia* (*R. amoeboides*) was founded by Fisch (*op. cit.*, p. 41), for an organism inhabiting *Lemna*. The zoospore was said to penetrate the cell of the host by its flagella. Inside, the thallus was amoeboid for a time, then surrounded itself with a wall, enlarged, and became a sporangium very similar to that formed by *Olpidium Lemnae*. After discharge the anteriorly uniflagellate zoospores from these sporangia often conjugated in pairs. The zygote eventually penetrated a *Lemna* cell and inside became transformed into a brownish thick-walled resting cell with from one to three or more large globules. This cell upon germination formed zoospores in an evanescent vesicle. Fischer (1892:28) considers *R. amoeboides* synonymous with *O. Lemnae*.

PRINGSHEIMIELLA COUCH

J. Elisha Mitchell Sci. Soc., 55:409. 1939

"Obligate endophytic parasites on Saprolegniaceae. Thalli from zoospores multiplying in host hyphae. Zoosporangial sori formed in the ends of host hyphae and resembling in superficial appearance and development the host zoosporangia. Sporangia globose or polygonal from pressure, each sporangium with an emergence papilla. Zoospores posteriorly uniflagellate, very minute. Resting bodies unicellular, spherical, brownish when mature, one to several formed within a larger polygonal or irregularly shaped cell. Zoosporangial and resting spore membranes bluish purple with chlor-iodide of zinc" (Couch, *loc. cit.*).

In hyphae of aquatic Phycomycetes.

Erected to accommodate a true chytrid, first seen by Pringsheim (1860), which has a superficial resemblance in the zoosporangial stage to *Woronina polycystis*.

PRINGSHEIMIELLA DIOICA Couch

J. Elisha Mitchell Sci. Soc., 55:410, pl. 49. 1939

"Infection by zoospores which leave cyst on host wall. Thalli from zoospores multiplying in host hyphae and carried by plasma currents of host to the distal parts of hyphae. Sporangia formed in cylindrical compartments, the latter resembling in shape, size, and position the sporangia of the host. Compartments separated from

healthy host hypha by cross wall. Each sporangium in a sorus developing from a separate thallus and forming an emergence papilla upon maturity. Sporangia spherical to oval or polygonal from pressure, 16-21 μ thick, with a cellulose membrane. Zoospores very minute, 1.8-3 \times 3 μ , spherical or slightly elongated, with one minute glistening globule, and a single posterior flagellum, moving directly away after a brief pause at the sporangial mouth. Resting bodies (zygotes) formed only where two sexually opposite or sexually compatible strains are brought together, spherical, 15-17 μ thick, golden brown with an eccentric globule and a minutely rough or reticulate membrane, formed within a larger cell which is polygonal from pressure. Containing cell 25-30 μ thick; sometimes larger and containing as many as six zygotes. Germinating by uniflagellate zoospores after six weeks' rest" (Couch, *loc. cit.*).

Parasitic in *Achlya dioica*, Pringsheim (1860:211, pl. 23, figs. 1-5), GERMANY; *Achlya* sp., *A. flagellata*, coll. J. N. and A. B. Couch, Ward, Shanor, UNITED STATES.

The species is dioecious, resting spores being formed only in cultures containing compatible or sexually opposite strains.

PLEOTRACHELUS Zopf

Nova Acta Acad. Leop.-Carol., 47:173. 1884

(Figure 5E, p. 78)

Thallus endobiotic, holocarpic, without a specialized vegetative system, unwalled at first, with pseudopodia, forming the rudiment of the zoosporangium at maturity, causing hypertrophy of the host; zoosporangium inoperculate, lying free in the host cell, with many (rarely from one to two) discharge tubes; zoospores posteriorly uniflagellate, formed in the sporangium; resting spore not (?) observed.

In Phycomycetes and algae.

Petersen (1905) has included in this genus a number of *Pleotrichelus*-like forms found by him in marine algae in Denmark. Some of these have upon later investigation (Sparrow, 1934c, 1936b) been found to possess biflagellate zoospores and have been referred either to *Petersenia* or to *Olpidiopsis*. Further work may establish the fact that the remainder of these marine fungi should be segregated from *Pleotrichelus*.

A spherical thick-walled resting spore which produces zoospores upon germination has been figured by Morini (1913) in *Pleotrachelus Zopfianus*, but further observations are needed to confirm the occurrence of such resting structures in the genus.

KEY TO THE SPECIES OF PLEOTRACHELUS

Sporangia predominantly spherical; in *Pilobolus*

Typical sporangia bearing numerous discharge tubes... *P. fulgens*, p. 110

Typical sporangia bearing from one to two discharge tubes

P. Zopfianus, p. 111

Sporangia broadly oblong-cylindrical; in green algae... *P. Petersenii*, p. 111

PLEOTRACHELUS FULGENS Zopf

Nova Acta Acad. Leop.-Carol., 47:173, pl. 16, figs. 25-36. 1884; Beitr.

Physiol. Morph. niederer Organismen, 2:7, pl. 1, figs. 11-14, pl. 2, figs.

1-5, 7-8. 1892

(Figure 5 E, p. 78)

Sporangia from one to eighty in the host, causing a marked spherical, pyriform, or broadly fusiform swelling of the infected parts, exactly spherical, 6.5-250 μ in diameter, with a colorless or light-yellow or red to reddish-brown fairly stout cellulose wall and from one to thirty straight or somewhat crooked tapering radiating discharge tubes, all of which usually penetrate the host wall; zoospores 2.2-3 μ in diameter (up to 3.6 μ long when elongated), ovoid, the broader end anterior, with a small colorless refractive globule and several coarse granules, flagellum attached to the narrower end, escaping through the discharge tubes upon the dissolution of their apices and forming temporary groups, capable of amoeboid movement; resting spore not observed.

Parasitic in mycelium, gemmae, and suspensors of *Pilobolus crystallinus* var. *areolata*, *P. Kleinii*, GERMANY.

In Zopf's second account of the species (1892:7) the vegetative stage was described. His observations indicated that the fatty material of the host which was colored with carotene was absorbed by the amoeboid thallus. The contents of the maturing sporangium also appear from the figures to be orange red, but are evidently colorless at maturity, since the zoospores possess no pigmentation.

The chytrid was found to be parasitized by a monad, *Endobiella destruens* Zopf.

Considerable variation in the size of the sporangia and the number of discharge tubes was noted. The largest sporangia usually occurred singly, formed about a thousand zoospores, and had up to thirty discharge tubes; smaller ones contained fewer spores and discharge tubes, the smallest bearing only one or two tubes.

PLEOTRACHELUS ZOPFLIANUS Morini

Mem. R. Accad. Sci. Istituto Bologna, Ser. VI, 10:301, figs. 1-4. 1913

Sporangium spherical or subspherical, pale yellowish orange, 41-47 μ in diameter, with from one to two cylindrical discharge tubes; zoospores ovoid-pyriform, uniflagellate, 3-4 μ long; resting spore spherical, thick-walled, upon germination cracking open and liberating zoospores.

In the bicellular trophocysts of *Pilobolus Pirottianus*, ITALY.

Doubtfully distinct from *Pleotrachelus fulgens*.

PLEOTRACHELUS PETERSENII Lund

Bot. Tidsskrift, 41:241, fig. 1. 1930

Sporangium broadly oblong-cylindrical, straight or curved, 24-89 μ long by 9-28 μ in diameter, wall thin, smooth, colorless, with from one to six very narrow discharge tubes 5-11 μ (up to 25 μ) long; zoospores uniflagellate; resting spore not observed. (Modified from Lund.)

In *Oedogonium sp.*, DENMARK (S.).

A fungus with more tubular sporangia bearing inflated contorted branches has been tentatively identified with this species by Sparrow (1936a: 428, pl. 14, fig. 5). No zoospores were seen, and hence no positive identification could be made.

IMPERFECTLY KNOWN SPECIES OF PLEOTRACHELUS

? PLEOTRACHELUS INHABILIS H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):456,
fig. IV, 1-6

A collective species containing *Pleotrachelus* forms found in *Polysiphonia violacea* and *Polysiphonia elongata*.

Two main types of sporangia occur: (1) those living in tetrasporangia and tetraspores of *Polysiphonia violacea* and (2) those living in parietal cells of the cystocarp of *P. elongata*.

1. Sporangia formed in tetraspores of *Polysiphonia violacea* and assuming their shape: Sporangia with smooth colorless walls which stain violet with chloriodide of zinc, with one or more (usually two or three) somewhat prolonged discharge tubes, $30-45 \times 39-60 \mu$, of variable shape (if occurring in the tetrasporangium before formation of the tetraspores, somewhat regularly spherical and filling it or, in instances of multiple infection, spherical and grouped; if formed during division of the tetrasporangium into tetraspores, filling the two-celled or each of the four-celled [tetrasporic] structures); zoospores after formation moving within the sporangium and escaping individually, body ellipsoidal, $2-3 \mu$ in diameter, flagellation unknown; other characters unknown.

2. Sporangia parasitic in parietal cells of the cystocarp of *Polysiphonia elongata*: Sporangia of irregular rounded form, with a smooth wall, oily refringent contents, and from one to three discharge tubes; large specimens $40 \times 41 \mu$, discharge tube 22μ ; medium-sized ones $10 \times 29 \mu$.

In *Polysiphonia*, DENMARK.

The lobations on sporangia formed in the dyads of the tetrasporangia (Petersen, *op. cit.*, fig. IV, 1) indicate a relationship of these forms to *Petersenia*, where, if the zoospores are found to be biflagellate, they should be placed.

Other imperfectly known types in marine algae are described by Petersen (*op. cit.*, p. 464).

? PLEOTRACHELUS MINUTUS H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):451,
fig. II, 1-4

Sporangium of variable shape, spherical or elongate-cylindrical, with a smooth thin wall, largest $16-24 \times 12-16 \mu$, with from one to three discharge tubes 4μ long; host cell little hypertrophied.

In hairs of *Chorda filum*, DENMARK.

? PLEOTRACHELUS OLPIDIUM H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):455,
fig. III, 7-9

Sporangia one or more in a host cell, not filling the lumen nor causing hypertrophy, regularly more or less spherical, with a smooth colorless wall which does not react to chloriodide of zinc, 9-30 μ in diameter, with from one to three discharge tubes 9-24 μ long; zoospores not seen; resting spore borne singly and loosely in a structure not differing in shape or size from the zoosporangium, with a smooth thickened wall.

In *Ectocarpus confervoides* (coll. Börgesen), Petersen (*loc. cit.*), FARÖE ISLANDS; *Ectocarpus* sp., *E. confervoides*, *Furcellaria* (coll. K. Rosenvinge), *Akinetospora*, Petersen (*loc. cit.*), *Polysiphonia* sp., *Pylaiella littoralis*, Sparrow (1934c:19, pl. 4, figs. L, N), DENMARK.

? PLEOTRACHELUS PARADOXUS H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):459,
fig. IV, 7-8

Sporangium of variable shape, frequently irregular, sometimes more or less spherical, sometimes oblong, one or several in each host sporangium, when occurring singly filling the host structure, wall colorless, thin, smooth, turning violet with chloriodide of zinc, with one or several discharge tubes passing through the discharge pores of the host sporangium, causing thickening of the host wall; zoospores not observed.

In sporangia of *Rhizophydium discinctum*, coll. F. Börgesen, NORWAY.

? PLEOTRACHELUS RADICIS de Wildeman

Ann. Soc. Belge Micro. (Mém.), 17:23, pl. 3, figs. 20-25. 1893; *ibid.*, 19:70, pl. 2, figs. 23-35. 1895

Sporangium spherical or ovoid, wall colorless or slightly yellow, with a large number of conical or tubular, sometimes irregular, discharge tubes; zoospores and resting spore not observed.

Three forms are distinguished:

1. Forma *major*, tubes numerous, wall colored, 65–85 μ in diameter. In roots of *Thlaspi arvense*, BELGIUM.

2. Forma *intermedia*, tubes rather numerous, wall very slightly colored and little thickened, 35–52 μ in diameter. In tissues of aquatic plants, SWITZERLAND.

3. Forma *minor*, tubes less numerous, rather slender, wall very slightly colored and little thickened, 17–26 μ in diameter. In tissues of aquatic plants ("vegetable debris"), SWITZERLAND.

Because of the shape and ornamentation of the sporangium and the central "spherule" with a more refractive portion in the contents, these structures strongly resemble the oöspores of an *artotrogus* type of *Pythium*.

? PLEOTRACHELUS ROSENVINGII H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):453,
fig. III, 1–6

Sporangia barrel-shaped when occurring singly, 20–25 μ in diameter, nearly filling the swollen host cell, spherical and not filling the host cell when there are several (up to six), with from one to three discharge tubes 4–25 μ long by 4–5 μ in diameter; zoospores ellipsoidal or pyriform, 2–3 μ long, with a single anterior flagellum.

Two different forms are included under this species:

1. Sporangia colorless, filling or nearly filling the host cell, 20–68 μ long by 24–41 μ in diameter, with from one to three short discharge tubes; zoospores not seen.

2. Sporangia filling or only partly filling the host cell, spherical if only partly filling it, with faint yellow contents and walls, showing little or no reaction to chloriodide of zinc, 10–31 μ long by 18–36 μ in diameter; zoospores elliptical or pyriform, 2–3 μ long, with a single anterior flagellum.

In *Pylaiella littoralis*, H. E. Petersen (*loc. cit.*), Sparrow (1934c:19, pl. 4, fig. M), DENMARK; (coll. A. Jessen) Petersen (*loc. cit.*), GREENLAND.

The zoospores will, upon further investigation, probably be found to be biflagellate; if they are, the fungus should be referred to *Petersenia* or *Olpidiopsis*.

? PLEOTRACHELUS (?) ROTATORIORUM Scherffel

Abstracts of Communications, V Inter. Bot. Congress, Cambridge, 1930:222;
Arch. Protistenk., 73:139, pl. 9, fig. 1. 1931

Sporangium spherical to broad-oval, colorless, smooth- and thin-walled, $44-55 \mu$ long by 51μ wide, with three discharge tubes nearly as long (4.4μ) as wide (6.6μ) and not extending beyond the host wall; zoospores not observed.

In egg of *Anuraea cochlearis* (?), HUNGARY.

PLASMOPHAGUS DE WILDEMAN

Ann. Soc. Belge Micro. (Mém.), 19:223. 1895
(Figure 5K, p. 78)

Thallus endobiotic, causing hypertrophy (swelling and elongation) of the host cell, plasmodial at first, later walled, holocarpic, without rhizoids; sporangium inoperculate, nearly filling the host cell, its wall distinct; zoospores posteriorly uniflagellate, with a single globule, discharged individually through a pore formed at the tip of a single short sessile (not projecting) papilla; resting spore not observed.

Whether or not the genus is distinct from *Olpidium* is a matter for further investigation. That the thallus nearly completely fills the host cell, that it lacks a definite discharge tube, and that it causes hypertrophy of the infected cell are all characteristics exhibited by one or another undoubted species of *Olpidium*. In these respects *Plasmophagus* also resembles species of *Rozella*. However, it differs from *Rozella* in that the walls of host and parasite are distinct, not fused.

PLASMOPHAGUS OEDOGONIORUM DE WILDEMAN

Ann. Soc. Belge Micro. (Mém.), 19:223, pl. 8, figs. 1-9, pl. 9, figs. 1-9. 1895

Sporangium saclike and somewhat irregular, almost completely filling the swollen and elongated algal cell, $20-23 \mu$ long by $8-11 \mu$ broad (in *Tribonema*), wall thin, smooth, colorless, discharge papilla lateral, small, just penetrating the host wall; zoospores ovoid or obovoid, 3μ long by 2μ wide, with a colorless eccentric globule and a flagellum; resting spore not observed.

Parasitic in filaments of *Oedogonium sp.*, de Wildeman (*loc. cit.*), FRANCE; *Tribonema bombycinum*, Sparrow (1933c:513, fig. I, 1), UNITED STATES.

No measurements are given by de Wildeman and those contained in the description above refer to the organism in *Tribonema*. It is probable that the parasite of *Oedogonium* attained larger dimensions, but this is only conjecture.

ROZELLA CORNU

Ann. Sci. Nat. Bot., V, 15:148. 1872

(Figure 5 F-I, p. 78; Figure 7, p. 122)

Rozia Cornu, Bull. Soc. Bot. France, 19:71. 1872. Non *Rozea* Bescherelle, Mém. Soc. Nationale Sci. Nat. Cherbourg, 16:241. 1871-72.
Pleolpidium Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4):43. 1892.

Thallus endobiotic, holocarpic, at first naked and indistinguishable from the host contents, later walled, at maturity forming either the rudiment of the sporangium, the wall of which is fused with that of the hypertrophied host (except when intercalary), or the resting spore; sporangium inoperculate, thin-walled, smooth, with one or more discharge papillae; zoospores formed in the sporangium, posteriorly uniflagellate, often with a single globule; resting spore endobiotic, thick-walled, smooth or spiny, apparently asexually formed, lying loosely in the swollen, sometimes walled-off, portions of the host, upon germination functioning as a sporangium.

The taxonomic status of *Pleolpidium* has been recently discussed in detail (Sparrow, 1938b).

The observations of Foust (1937) on *Rozella Allomycis* indicate that in some (but not all) specimens a single thallus may not only completely fill an infected part, but may also sometimes segment and, as in *R. septigena*, form several sporangia. If this segmentation is clearly shown not to be due to multiple infection then the diagnosis above should be modified to include this sorus formation, or a new genus should be erected for *R. septigena* Cornu and *R. Allomycis*. Germination of the spiny resting spores has been secured by Foust and reinfection by means of the zoospores has been observed. These formed the typical sporangial stage, proving unquestionably that the two phases are related.

Butler has concluded from observations on a number of species that in some instances at least the plasma from several spores may unite in the host to form a true plasmodium, from which a single sporangium may arise. He does not exclude, however, the possibility that one thallus has gained the ascendancy and developed at the expense of the rest.

The species are all parasitic in the hyphae and reproductive organs of other aquatic Phycomycetes. It has been customary to consider one species to be restricted to a single host genus, but this supposition awaits the confirmation of convincing experimental evidence.

KEY TO THE SPECIES OF ROZELLA¹

Parasitic in fresh-water Phycomycetes

Parasitic in filamentous Phycomycetes

Parasitic in the host sporangia or, if in the hyphae, occurring singly, not in linear series

Parasitic in the hyphae of *Monoblepharis*

R. Monoblepharidis-polymorphae, p. 118

Parasitic in the sporangia of *Araiopora*... *R. Rhipidii-spinosi*, p. 118

Parasitic in the sporangia and immature resting spores of

Blastocladia *R. Blastocladiae*, p. 119

Parasitic in the sporangia of *Apodachlya*

R. Apodyae-brachynematis, p. 119

Parasitic in *Pythium*

Parasitic in the sporangia of the host; resting spore

smooth *R. cuculus*, p. 119

Parasitic in the hyphae of the host; resting spore spiny

R. irregularis, p. 120

Parasitic in the hyphae of the host, forming a linear series of sporangia

Parasitic in *Achlya* and *Saprolegnia* *R. septigena*, p. 120

Parasitic in *Allomyces* *R. Allomycis*, p. 121

Parasitic in members of the Chytridiales or Lagenidiales

Parasitic in prosporangia of *Polyphagus* *R. Polyphagi*, p. 123

Parasitic in cells of *Lagenidium* and *Myzocytium*

R. pseudomorpha, p. 124

Parasitic in marine fungi; in sporangia of *Chytridium Polysiphoniae*

R. marina, p. 124

¹See also Karling, *Torreya*, 41:105-108. 1941; *Amer. J. Bot.*, 29:24-35. 1942. Species parasitic in *Cladochytrium*, *Endochytrium*, *Rhizophlyctis*, *Pythium*, and *Phytophthora* are described in these two papers.

ROZELLA MONOBLEPHARIDIS-POLYMORPHAE Cornu

Ann. Sci. Nat. Bot., V, 15:150, pl. 4, figs. 13-18. 1872

Pleolpidium Monoblepharidis (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):44. 1892.

Sporangium formed in intercalary swollen parts of the hyphae, ovoid, the lateral walls fused with those of the host, with a single small lateral discharge pore; zoospores not observed; resting spore spherical, brown, the thickened wall densely covered with tenuous spines, in intercalary or lateral swellings of the host hyphae, germination not observed.

Parasitic in *Monoblepharis polymorpha*, Cornu (*loc. cit.*), FRANCE; Laibach (1927), GERMANY.

ROZELLA RHIPIDIIS-SPINOSI Cornu

Ann. Sci. Nat. Bot., V, 15:153, pl. 5, figs. 1-9. 1872

Pleolpidium Rhipidiis (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):44. 1892.

Pleolpidium Araiosporae (Cornu) Minden, Kryptogamenfl. Mark Brandenburg, 5:252. 1911 (1915).

Sporangium completely filling the abnormally swollen and obpyriform sporangium of the host, with a prominent apical papilla; zoospores variable in shape, reniform, spherical, or ellipsoidal, with a long posterior flagellum, discharged through a broad pore, resting a few seconds at the orifice before swimming away; resting spore spherical, yellowish brown or reddish, with dense contents, wall slightly thickened, covered with tenuous spines, germination not observed, predominantly formed in the spiny sporangia of the host.

Parasitic in smooth and spiny sporangia of *Araiospora spinosa*, FRANCE.

Cornu noted that the sporangial stage of the parasite was predominantly formed in the smooth sporangia of the host, the resting spores, in the spiny sporangia. The fungus developed extensively in his cultures and prevented the making of a complete study of the *Rhipidium* (*Araiospora*).

ROZELLA BLASTOCLADIAE (Minden) Sparrow

Mycologia, 30:377. 1938

Pleolpidium Blastocladiae Minden, Kryptogamen-Fl. Mark Brandenburg, 5:253. 1911 (1915); Falck, Mykolog. Untersuch. Berichte, 2(2):pl. 4, fig. 33. 1916.

Sporangium assuming the shape of the hypertrophied host sporangium, which becomes somewhat broader and more ovoid than normal, with an apical pore, collapsing after discharge of the zoospores; zoospores not observed; resting spore exactly spherical, brown, thick-walled, the exospore densely covered with tenuous spines, germination not observed.

Parasitic in sporangia and immature resting spores (?) of *Blastocladia Pringsheimii*, Minden (*loc. cit.*), Laibach (1927:624), GERMANY; Thaxter (1896a:50), UNITED STATES; H. E. Petersen (1909:424, fig. 26 c-d; 1910:555, fig. 26 c-d), DENMARK.

ROZELLA APODYAE-BRACHYNEMATIS Cornu

Ann. Sci. Nat. Bot., V, 15:161, pl. 5, figs. 10-14. 1872

Pleolpidium Apodyae (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):45. 1892.

Sporangium filling the sporangium of the host and assuming its shape, with a small apical papilla; zoospores somewhat elongate, with a posterior flagellum, escaping through a small pore resulting from the dissolution of the papilla; resting spore formed in the sporangium of the host, spherical, somewhat thick-walled, brownish(?), covered with very short tenuous spines.

Parasitic for the most part in the terminal segments (sporangia) of *Apodachlya brachynema*, FRANCE.

Plants of *Araiopora* occurring in the same tufts as the *Apodachlya* were not infected by the zoospores of *Rozella Apodyae-brachynematis*. The spines on the resting spore are noticeably shorter than those of *R. Rhipidii-spinosi*.

ROZELLA CUCULUS (Butler) Sparrow

Mycologia, 30:377. 1938

Pleolpidium cuculus Butler, Mem. Dept. Agr. India, Bot. Ser., 1:125, pl. 7, figs. 22-25. 1907.

Sporangium spherical; subspherical, or pyriform, formed in the sporangium of the host or in pronounced intercalary swellings of the hyphae, $19.2-24 \mu$ in diameter, with a single papilla; zoospores obclavate, clavate, or ovoid, the flagellum emerging from the broader end; resting spore spherical, single, free in the sporangium or intercalary swelling of the host, $12-18 \mu$ in diameter, with a smooth pale-yellow somewhat thickened wall, germination not observed.

Parasitic in sporangia of *Pythium intermedium*, Butler (*loc. cit.*), IRELAND, FRANCE; hyphae of *Pythium monospermum*, Tokunaga (1933b:82, pl. 5, fig. 12), JAPAN.

Pleolpidium tuberculorum Vuillemin (1909) should perhaps be included under this species. It differs from Butler's fungus only in having slightly larger and fewer zoospores and somewhat larger resting spores ($17.5-23 \times 15.4-20 \mu$). It was found in France parasitic in the sporangia of *Pythium*.

Chytridium simulans Dangeard (1896-97:21, fig. 1), occurring in terminal or lateral swellings on *Pythium*, may be referable to *Rozella cuculus*. The resting spores, however, were not observed.

ROZELLA IRREGULARIS (Butler) Sparrow

Mycologia, 30:377. 1938

Pleolpidium irregulare Butler, Mem. Dept. Agr. India, Bot. Ser., 1:123, pl. 8, figs. 1-12. 1907.

"Sporangia formed in the hyphae of the host, irregular in shape, terminal and intercalary, averaging 23μ in diameter, with a single papilla; zoospores obclavate, with a single cilium borne posteriorly; durable spores single, free in the cavity of the host-filament which is enlarged to contain them, numerous, $11-15 \mu$ in diameter, spherical, of a pale yellow colour, with a moderately thick wall, provided with short regular spines; germination not observed" (*Butler, loc. cit.*).

Parasitic in *Pythium* (?) *vexans*, ENGLAND.

ROZELLA SEPTIGENA Cornu

Ann. Sci. Nat. Bot., V, 15:163, pl. 6. 1872. Non Fischer, Jahrb. wiss. Bot., 13:321, pl. 14, fig. 19, pl. 15, figs. 20-28. 1882
 (Figs. 5 H-I, p. 78)

Sporangia possibly formed by successive fractionation of one thallus, in transversely or obliquely walled-off segments of the some-

times slightly swollen host hyphae which they completely fill, with from one to several discharge papillae; zoospores minute, numerous, arched, posteriorly uniflagellate, without globules; resting spore spherical, with a slightly thickened wall covered with short tenuous spines, brownish, with dense contents, formed in spherically swollen short lateral branches of the hyphae, which are continuous with the main axis or separated by a cross wall, germination not observed.

Parasitic in *Achlya racemosa*, *A. polyandra*, *Saprolegnia spiralis*, Cornu (*loc. cit.*), FRANCE; *Saprolegnia dioica*, Pringsheim (1860:205, pl. 22, figs. 1-6), GERMANY.

The fungus of Sorokin (1883:25, fig. 25) in *Achlya racemosa* in European and Asiatic Russia was said to form small uniflagellate zoospores and larger biflagellate ones. Cornu observed a similar phenomenon, but attributed the occurrence of the large spores to poor environmental conditions. Sparrow (1932b:273; 1936a:425) has recorded this species from the United States and England, but no zoospores were observed and the identifications are therefore subject to doubt.

Cornu's name has been applied, in error, by Fischer (1882:365) to a similar-appearing parasite in *Saprolegnia* which forms biflagellate zoospores. The findings of Foust (1937) in *Rozella Allomycis* indicate strongly that Cornu's observations on the uniflagellation of the zoospores of his parasite are correct.¹ If fractionation of the thallus in this species and the following one is definitely proved to occur after infection by a single zoospore, they should be removed from *Rozella* and placed in a new genus.²

Pringsheim, who, incidentally, figures zoospores killed with iodine as uniflagellate, considered the fungus to be the antheridia of the *Saprolegnia*.

ROZELLA ALLOMYCIS Foust

J. Elisha Mitchell Sci. Soc., 53:198, pls. 22-23. 1937
(Figure 7, p. 122)

Sporangia filling the more distal parts of the host hyphae, developing linearly, from one to five in basipetal succession, generally barrel-shaped, 20-40 μ long by 12-20 μ in diameter (usually 24.6 \times 15.9 μ),

¹ See *Rozellopsis* Karling, Amer. J. Bot., 29:33. 1942.

² See also *Rozella Achlyae* Shanor, J. Elisha Mitchell Sci. Soc., 58:100. 1942.

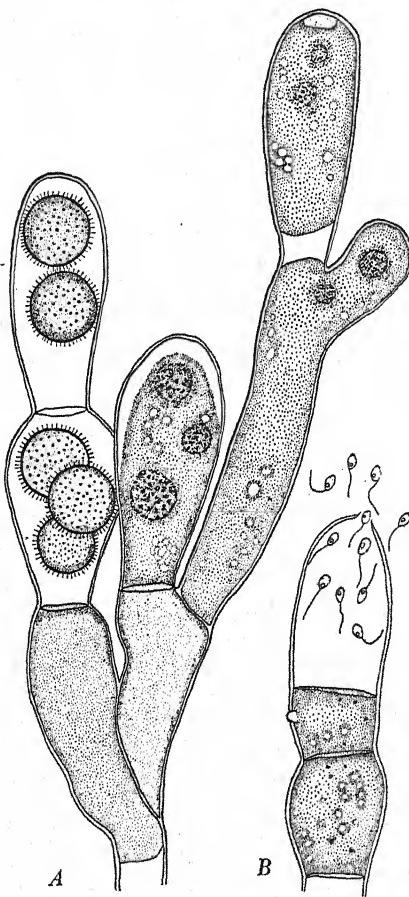


FIG. 7. *Rozella Allomycis* Foust parasitic in *Allomyces*

A. Tip of parasitized plant, showing (left) mature resting spores in zoosporangia of host and (right) immature thalli in zoosporangia and hyphae of host. B. Discharging sporangium of parasite; at least two sporangia have been formed in a single sporangium of *Allomyces*.

(Drawn by V. M. Cutter, Jr.)

occasionally divided by one or more partitions into several smaller sporangia, usually with one discharge papilla 1.3μ long; zoospores ovoid, the broader end anterior, $3-4 \mu$ wide, having a single globule, with a posterior flagellum 16μ long; resting spores formed behind the

sporangia in from one to thirty-five swollen spherical, subspherical, barrel-shaped, nearly cylindrical, or irregular segments 20–70 μ long by 20–40 μ in diameter, each segment containing from one to sixteen yellow to reddish-brown resting spores, the latter spherical, 12–20 μ in diameter (average 15.9 μ) including the spines, with a thick (1.5 μ) wall covered by slender long (1.3 μ) spines, contents with a central hyaline globose mass surrounded by granular protoplasm, upon germination functioning as a sporangium, the uniflagellate zoospores eventually forming new sporangia. (Modified from Foust.)

Parasitic in *Allomyces arbusculus*, Foust (*loc. cit.*), *A. javanicus*, Sparrow (TEXAS), UNITED STATES; *A. arbusculus*, F. T. Wolf (1941: 170), BRAZIL, ARGENTINA; *Allomyces* sp., coll. C. D. LaRue, NICARAGUA.

Germination of the resting spores, which, either wet or dry, retain their vitality for several months, was secured after a rest period of only a week when new water and fresh young *Allomyces* plants were added to the culture.

Miss Foust was unable to find evidences of a separate wall produced by the parasite. She noted that some sporangial rudiments laid down one or more partitions within the primary segment which were horizontal, vertical, or at angles to the original septa. If these septations should be clearly shown to be the result of only a single infection they would be of great interest, as has been indicated elsewhere (see p. 121).

The "Rozella Allomycetes" mentioned by Nabel (1939:527), but not described, probably belongs here.

ROZELLA POLYPHAGI Sparrow

J. Linn. Soc. London (Bot.), 50:426, pl. 14, figs. 19–20. 1936
(Figure 5 F–G, p. 78)

Pleolpidium Polyphagi Sparrow, Trans. Brit. Mycol. Soc., 18:215. 1933.

Sporangium colorless, spherical, completely filling the often markedly swollen prosporangium of the host, 20–48 μ in diameter, possessing at maturity from two to six prominent papillae 4–8 μ in diameter, through which the innumerable minute posteriorly uniflagellate narrowly ovoid zoospores 2–3 μ long by 1.5–2 μ in diameter, with a single globule, are discharged; resting spore not observed.

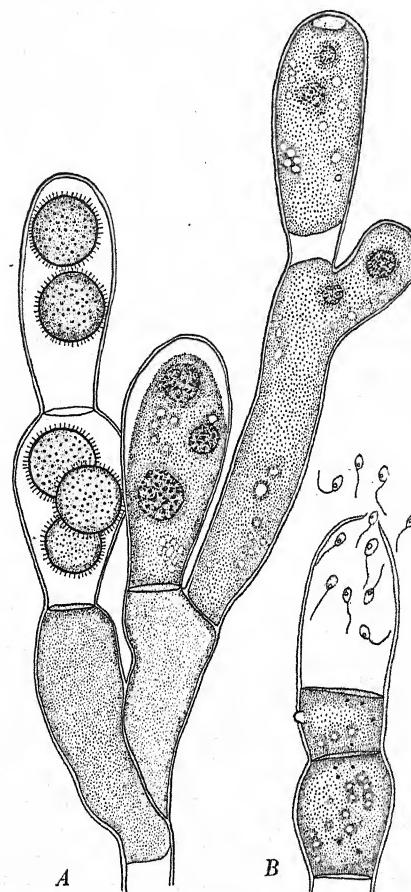


FIG. 7. *Rozella Allomycis* Foust parasitic in *Allomyces*

A. Tip of parasitized plant, showing (left) mature resting spores in zoosporangia of host and (right) immature thalli in zoosporangia and hyphae of host. B. Discharging sporangium of parasite; at least two sporangia have been formed in a single sporangium of *Allomyces*.

(Drawn by V. M. Cutter, Jr.)

occasionally divided by one or more partitions into several smaller sporangia, usually with one discharge papilla 1.3μ long; zoospores ovoid, the broader end anterior, $3-4 \mu$ wide, having a single globule, with a posterior flagellum 16μ long; resting spores formed behind the

sporangia in from one to thirty-five swollen spherical, subspherical, barrel-shaped, nearly cylindrical, or irregular segments 20–70 μ long by 20–40 μ in diameter, each segment containing from one to sixteen yellow to reddish-brown resting spores, the latter spherical, 12–20 μ in diameter (average 15.9 μ) including the spines, with a thick (1.5 μ) wall covered by slender long (1.3 μ) spines, contents with a central hyaline globose mass surrounded by granular protoplasm, upon germination functioning as a sporangium, the uniflagellate zoospores eventually forming new sporangia. (Modified from Foust.)

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Miss Foust was unable to find evidences of a separate wall produced by the parasite. She noted that some sporangial rudiments laid down one or more partitions within the primary segment which were horizontal, vertical, or at angles to the original septa. If these septations should be clearly shown to be the result of only a single infection they would be of great interest, as has been indicated elsewhere (see p. 121).

The "Rozella *Allomyctes*" mentioned by Nabel (1939:527), but not described, probably belongs here.

ROZELLA POLYPHAGI Sparrow

J. Linn. Soc. London (Bot.), 50:426, pl. 14, figs. 19–20. 1936
(Figure 5 F–G, p. 78)

Pleolpidium Polyphagi Sparrow, Trans. Brit. Mycol. Soc., 18:215. 1933.

Sporangium colorless, spherical, completely filling the often markedly swollen prosporangium of the host, 20–48 μ in diameter, possessing at maturity from two to six prominent papillae 4–8 μ in diameter, through which the innumerable minute posteriorly uniflagellate narrowly ovoid zoospores 2–3 μ long by 1.5–2 μ in diameter, with a single globule, are discharged; resting spore not observed.

Parasitic in prosporangia of *Polyphagus Euglenae*, ENGLAND.

Scherffel (1925b:6, pl. 1, fig. 10) has observed in the prosporangia of *Polyphagus parasiticus* a brownish rough-walled resting structure. Though the structure may be the resting spore of *Rozella Polyphagi* the presence on it of a delicate rhizoid makes this improbable.

ROZELLA PSEUDOMORPHA (Scherffel), comb. nov.

Olpidium (?) pseudomorphum Scherffel, Arch. Protistenk., 54:510, pl. 28, figs. 1-5. 1926.

Sporangium filling the vegetative cell of the host, and hence assuming its shape and size, forming a fairly stout tapering discharge tube; zoospores narrowly ellipsoidal, ovoid, or plump and rodlike, somewhat arched, with from three to five refractive granules, flagellum fairly long, trailing, attached at the concave side of the body, zoospores emerging individually from the discharge tube and remaining for a time near the orifice undergoing amoeboid change of shape, movement hopping; resting spore unknown.

Parasitic in vegetative cells of *Lagenidium Rabenhorstii*, HUNGARY.

A fungus also considered to be this species was found by Scherffel (*loc. cit.*) in vegetative cells of *Myzocytium proliferum*. It differed from the *Lagenidium* parasite only in the fact that the zoospores had a single basal refractive droplet and exhibited a swimming, not a hopping, type of movement.

Because of the fact that the fungus completely fills the host cell it is referred to *Rozella*, even though the formation of a pronounced discharge tube appears rare among members of the genus.

ROZELLA MARINA Sparrow

Biol. Bulletin, 70:256, text figs. 32-33. 1936

Pleolpidium marinum Sparrow, *loc. cit.*

Sporangium spherical, completely filling the enlarged host sporangium, 30-45 μ in diameter, at maturity forming from one to three pores, through which the zoospores are discharged; zoospores ellipsoidal, 3 μ long by 2 μ in diameter, posteriorly uniflagellate, without globules; resting spore not observed.

Parasitic in the sporangia of *Chytridium Polysiphoniae*, UNITED STATES.

EXCLUDED SPECIES OF ROZELLA

* ROZELLA ALLOMYCETES Nabel, nom. nud.

Archiv f. Mikrobiol., 10 (4): 527. 1939

A name unaccompanied by a description. Probably referable to *Rozella Allomyces* Foust.

* PLEOLPIDIUM INFLATUM Butler¹

Mem. Dept. Agr. India, Bot. Ser., 1: 126, pl. 7, figs. 17-21. 1907

"Sporangia spherical, oval or pyriform, formed in the spores of the host which, with the supporting hyphae, are greatly swollen, up to 85 μ in diameter, with one or more papillae; zoospores very numerous, elongated, unequilateral, with two cilia, one in front and the other lateral near the back; durable spores not seen" (Butler, *loc. cit.*).

Parasitic in *Pythium intermedium*, Butler (*loc. cit.*), *Pythium* sp., Sparrow, FRANCE; *Phytophthora cryptogea*, *P. megasperma*, Waterhouse (1940:7, figs. 1-8), ENGLAND.

Although the fungus superficially resembles a species of *Rozella*, the biflagellate character of the zoospore allies it to *Olpidiopsis* or possibly to *Pseudolpidium*. A recent study by Waterhouse (1940) has confirmed the biflagellate character of the zoospore. Observations on the nature of the resting spore will be necessary before the affinities of *Pleolpidium inflatum* can be determined. The incompletely known fungus on *Phytophthora* noted by Barrett (1934) is a *Rozella*.

* ROZELLA SEPTIGENA Cornu²

Sensu Fischer, Jahrb. wiss. Bot., 13: 365, pl. 14, fig. 19, pl. 15, figs. 20-28. 1882.
Non sensu Cornu, Ann. Sci. Nat. Bot., V, 15: 163. 1872

Sporangia and their method of formation like those of *Rozella septigena* Cornu; zoospores narrowly ovoid, laterally biflagellate, 6-8 μ long by 4 μ broad; resting spores in swollen lateral branches of host, spherical, 20 μ in diameter; wall brown, covered by tenuous

¹ The species was described by Butler as a doubtful member of *Pleolpidium* Fischer (= *Rozella* Cornu). See *Rozellopsis inflata* (Butler) Karling, Amer. J. Bot., 29: 33. 1942.

² See Karling, *loc. cit.*; Mycologia, 34: 206. 1942.

spines 2μ long, contents with a large oil globule, germination not observed.

Parasitic in hyphae of *Saprolegnia sp.*, not capable of infecting *Achlya*, Fischer (*loc. cit.*), Minden (1915:272), GERMANY.

The septate plasmodium is here known to arise from a single zoospore infection.

* ROZELLA SIMULANS Fischer

Jahrb. wiss. Bot., 13:365. 1882

Like the preceding fungus, but said to be confined to *Achlya*. Sporangia 60–250 μ long by 25–90 μ in diameter; zoospores narrowly ellipsoidal or cylindrical, $6 \times 2.4 \mu$, with two anterior unequal flagella; resting spore spiny.

In *Achlya polyandra*, *A. racemosa*, Fischer (*loc. cit.*), Minden (1915:273) (including resting spores), GERMANY; *Achlya*, Maurizio (according to Minden, 1915:273), ITALY; *Achlya flagellata*, Tokunaga (1933a:25), JAPAN.

These two fungi should be carefully restudied and placed in a genus of their own.

IMPERFECTLY KNOWN GENERA OF THE OLPIIDIACEAE

? BLASTULIDIUM Pérez

C. R. Soc. Biol., 55:715, figs. A–E. 1903

? BLASTULIDIUM PAEDOPHTHORUM Pérez

Loc. cit.

Thallus endobiotic, with a thin wall, ellipsoidal, 25μ long by 20μ in diameter, or consisting of a few cells with short rudimentary branches; sporangium inoperculate, formed from the whole thallus or its segments; zoospores ovoid, with one long axillary flagellum, formed in the sporangium, where motion is initiated, and escaping from it through a short neck; resting spore (?) citriform, with a thickened wall, germination not observed.

Parasitic in eggs and embryos of various Crustacea, *Daphnia obtusa*, *Simocephalus vetulus*, *Chydorus sphaericus*, *Lynceus*, larvae of *Corethra* (gnat), Pérez (*loc. cit.*), Chatton (1908:34), FRANCE.

Pérez considered the organism a haplosporidian (Protozoa), but Chatton, after noting the flagellation of the spore, referred it to the chytrids, particularly to *Olpidium* and *Synchytrium*.

The genus is a puzzling one, and, since no clear picture of it is given by either Pérez or Chatton and the term "axillary" does not indicate to what pole of the spore the flagellum is attached, it will remain so until new observations of a purely morphological nature are made. It may be related to *Septolpidium*.

Blastulidium was considered distinct from *Olpidium* by Chatton because of the formation of a large central vacuole and the fact that the thallus was occasionally septate and yeastlike.

Pérez described external ellipsoidal bodies adherent to the Crustacea as possibly representing the resting stage, but Chatton believed these to be single or conjugated zoospores which had fixed themselves on the animal, infected it, and developed. The resting stage observed by Chatton consisted of a thick-walled citriform structure, which he conjectured was probably formed after the parasite quit the dead host, moved amoeboidly away, and encysted.

? CHYTRIDHAEMA MONIEZ

C. R. Acad. Sci. Paris, 104:183. 1887

? CHYTRIDHAEMA CLADOCERARUM Moniez

Loc. cit.

Sporangium inoperculate, a flattened sac without cross walls or a discharge tube, formed within the body cavity of the host; zoospores top-shaped, 3μ long, with dense contents, bearing a refractive protuberance on the broad base, the opposite extremity prolonged into a flagellum, many formed in a sporangium.

Parasitic in Crustacea, *Sinocephalus retulus*, *Acroperus leucocephalus*, FRANCE.

Little of taxonomic significance can be obtained from the description. The sporangia are said to fill the body cavity of the animal, whereas the zoospores were found in abundance in the blood. It is not definitely stated whether the flagellum is anterior or posterior. Moniez thought the organism resembled olpidiaceous and lagenidiaceous fungi. He considered that the protuberance on the zoospore

was a sort of antheridium and that the sporangia were formed by the whole mycelium of a chytrid.

EXCLUDED GENUS OF THE OLPIDIACEAE

* ENDOLPIDIUM DE WILDEMAN

Ann Soc. Belge Micro. (Mém.), 18:153. 1894

* ENDOLPIDIUM HORMISCIAE de Wildeman

Loc. cit.

Differing from *Olpidium* only in forming a short discharge tube which does not penetrate the algal wall and in producing a hypertrophy of the host cell; zoospores and resting spores not observed.

On *Hormiscia zonata*, FRANCE.

ACHLYOGETONACEAE

Thallus endobiotic, holocarpic, becoming transversely septate at maturity and forming from two to several linearly arranged inoperculate sporangia, zoospores posteriorly uniflagellate; resting stage not known with certainty.

Occurring primarily in fresh-water algae.

The family differs from the Olpidiaceae in forming in linear series from the thallus two or more sporangia. Resting structures have not as yet been adequately demonstrated, although they have been reported as occurring in *Achlyogeton* (Martin, 1927) and *Bicricium*.

KEY TO THE GENERA OF THE ACHLYOGETONACEAE

Thallus forming typically a linear series of more than two sporangia

Zoospores encysting at the orifice of the discharge tube

ACHLYOGETON, p. 129

Zoospores clustering at, but eventually swimming directly away
from, the orifice of the discharge tube without encysting

SEPTOLPIDIUM, p. 132

Thallus forming two sporangia, which are separated by a more or less

well defined isthmus BICRICIUM, p. 133

ACHLYOGETON SCHENK

Bot. Zeitung, 17:398. 1859

(Figure 8 A-B, p. 130)

Thallus endobiotic, holocarpic, unbranched, without rhizoids, walled, at first tubular, later segmented and forming a chainlike series of cells each of which develops a discharge tube and becomes an inoperculate sporangium; zoospores posteriorly uniflagellate, with a refractive globule, escaping as separate bodies and forming a motionless group at orifice of discharge tube, encysting, emerging from the cellulose cysts after a period of rest and swimming away, the empty cysts persistent for a time; resting spore not (?) observed.

Parasites of green algae and eelworms.

The similarity in the body plan of *Achlyogeton* to that of *Myzocytium* has resulted in the former's usually being placed in the Lagenidiales rather than in the Chytridiales. This, as Butler (1928:820) has pointed out, has been a cause of difficulty to those attempting to discover the true affinities of these fungi. The flagellation of the spore marks it unquestionably as a member of the Chytridiales.

ACHLYOGETON ENTOPHYTUM Schenk

Bot. Zeitung, 17:398, pl. 13, fig. A, 1-8. 1859

(Figure 8 A-B, p. 130)

Sporangia from two to fifteen, strongly constricted at the stout cross walls, individuals ellipsoidal or subellipsoidal, 15-55 μ by 9.6-20.4 μ , wall smooth, slightly thickened, discharge tube arising at right angles to the long axis of the sporangium, fairly broad, generally expanded where it makes contact with the inner wall of the alga and prolonged outside for a varying distance (up to 60 μ); zoospores ovoid or broadly pyriform, with a colorless refractive basal globule, a vacuole, and a flagellum about three times as long as the body, emerging as elongate bodies upon the rupturing of the slightly expanded tip of the discharge tube and forming at the orifice a group of spherical cysts 4 μ in diameter, issuing from these after a period of rest and swimming away; resting spore possibly not as yet observed.

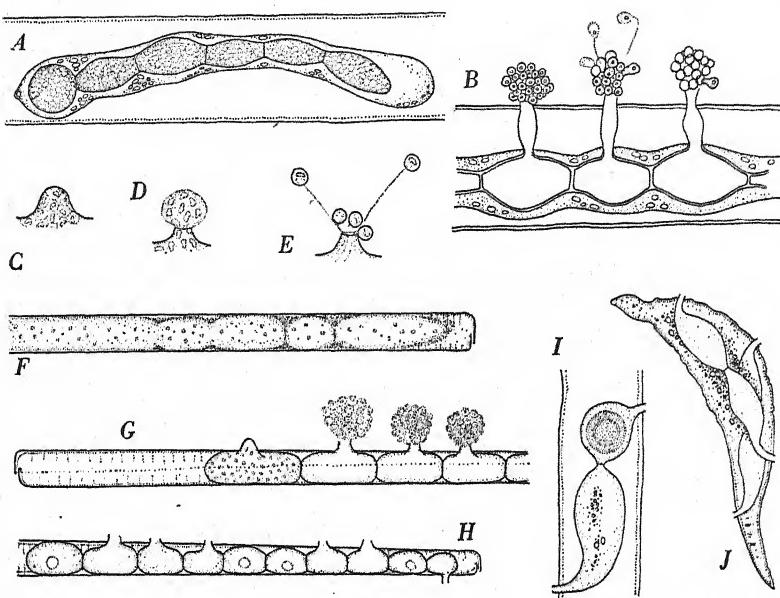


FIG. 8. Achlyogetonaceae

A-B. *Achlyogoton entophytum* Schenk (approx. $\times 500$) in filaments of *Cladophora*: A, thallus, showing segmentation into a linear series of zoosporangia; B, discharged zoosporangia with clusters of encysted zoospores at orifices of discharge tubes; in left-hand cluster zoospores are all encysted, in middle one they are emerging from cysts, and in right-hand group all but one have emerged, leaving the empty cysts behind. C-H. *Septolpidium lineare* Sparrow ($\times 400$) in diatoms: C, discharge papilla just before moment of discharge; D, first zoospores emerging en masse; E, zoospores swimming directly away from sporangium; this behavior is not usual, but is occasionally observed; F, immature thallus in diatom, showing progressive segmentation of tubular body into sporangia; G, group of sporangia produced from single thallus; sporangium on left has formed a papilla; remainder have discharged their zoospores, which form motionless clusters at orifices of discharge tubes; H, chain of empty sporangia. I-J. *Bicricium* ($\times 450$) in algae and eelworms: I, *Bicricium transversum* Sorokin, two-linked thallus in *Cladophora*; a resting structure is present in one segment; J, *Bicricium lethale* Sorokin, two pairs of empty sporangia in body of eelworm.

(A-B, Schenk, 1859a; C-H, Sparrow, 1936a; I-J, Sorokin, 1883)

In *Cladophora sp.*, Schenk (*loc. cit.*), GERMANY; "Confervacées," Sorokin (1883:38, fig. 48), ASIATIC RUSSIA; *Cladophora sp.*, Martin (1927:188, fig. 1), UNITED STATES; *Cladophora sp.*, Tokunaga (1934a: 227, fig. 1), JAPAN.

Sorokin (1876:63, pl. 3, figs. 2-5) has reported the species as occurring in *Anguillula* in European Russia. A further morphological study of this form is necessary before it can be considered identical with the alga inhabitant. It is certain from Sorokin's account that the typical encystment of the spores occurred after discharge. From his Plate 3, Figure 5, it is also evident that the sporangia which had thin cross walls were not simultaneously formed from the tubular thallus, but progressively, as in *Septolpidium*.

Both Martin and Tokunaga noted resting bodies associated with sporangia. As Tokunaga suggested, the round thick-walled resting cells observed by him, each of which was accompanied by a companion cell, were probably formed by a species of *Olpidiopsis* parasitizing the sporangia of the *Achlyogeton*. The resting cells found by Martin were possibly of similar origin, although in this instance either the companion cell had disintegrated or the spore was formed asexually.

IMPERFECTLY KNOWN SPECIES OF ACHLYOGETON

? ACHLYOGETON (?) ROSTRATUM Sorokin

Ann. Sci. Nat. Bot., VI, 4:64, pl. 3, figs. 40-45. 1876¹

Sporangia ten or more, slightly constricted at the thin cross walls, individuals ellipsoidal or somewhat irregular, 7-9 μ long by 5-6 μ wide, wall smooth, slightly thickened, discharge tube arising from the mid-region of the sporangium, long, often somewhat tortuous, expanded where it makes contact with the inner wall of the substratum and penetrating the latter with a short narrow tube; zoospores and resting spore not observed.

In *Anguillula*, Sorokin (*loc. cit.*), EUROPEAN RUSSIA; filaments of "Conferves," Sorokin (1883:38, fig. 49), EUROPEAN RUSSIA, ASIATIC RUSSIA.

Sorokin was uncertain of the generic disposition of his fungus. Fischer (1892) and Minden (1915) have supposed it to be a *Myzop-*

¹ See also Sorokin, *Revue Mycologique*, 11:188, pl. 81, fig. 119. 1889.

cytium, probably because of the presence of a swelling on the basal part of the discharge tube. The figure given in Sorokin's 1883 paper shows the thallus to be nearly devoid of constrictions.

? *ACHLYOGETON SALINUM* Dangeard

Le Botaniste, 24:240, pl. 24, figs. 1-3. 1932

Sporangia in chains of six or more, ellipsoidal, with a single discharge tube.

In *Cladophora sp.* (marine), FRANCE.

From the figures given, the fungus is very probably *Sirolpidium Bryopsidis*, which is occasionally found in *Cladophora*. Dangeard thinks it may be a species of *Myzocytium*, but this is unlikely since the thallus is successively divided into sporangia and since the zoospores are completely formed within the sporangium.

SEPTOLPIDIUM SPARROW

Trans. Brit. Mycol. Soc., 18:215. 1933; J. Linn. Soc. London (Bot.), 50:428. 1936

(Figure 8 C-H, p. 130)

Thallus endobiotic, cylindrical, unbranched, holocarpic, without a specialized vegetative system, at maturity successively divided by transverse walls into a series of conjoined segments, each of which becomes an inoperculate sporangium with a single evacuation tube through which the posteriorly uniflagellate zoospores are discharged; resting spore not observed.

A monotypic genus known thus far only in diatoms.

Septolpidium closely resembles *Achlyogeton* except that the zoospores lack an encysted stage (Fig. 8 C-E, G).

SEPTOLPIDIUM LINEARE Sparrow

Trans. Brit. Mycol. Soc., 18:215. 1933; J. Linn. Soc. London (Bot.), 50:428, text fig. 1. 1936

Thallus narrowly cylindrical, smooth-walled, with slightly tapering ends, 75-130 μ long by 5-12 μ in diameter, divided at maturity into a linear series of truncated conjoined sporangia; sporangia 8-37

μ long by 5-12 μ in diameter, each forming a single broad abruptly tapering evacuation tube 3-5 μ in diameter which protrudes from the host cell and through which the numerous zoospores are discharged; zoospores spherical, 3-4 μ in diameter, with from one to four spherical or irregularly shaped refractive granules, often forming upon emergence a spherical motionless temporary cluster at the mouth of the discharge tube, ultimately swimming away, sometimes assuming motility directly after emergence.

Parasitic in *Synedra sp.*, ENGLAND.

BICRICIUM SOROKIN

Arch. Bot. Nord France, 2:37. 1883 (separate)¹
(Figure 8 I-J, p. 130)

Thallus endobiotic, holocarpic, at maturity divided into two segments separated from each other by a narrow septate isthmus; sporangia inoperculate, one sporangium formed from each of the segments, each bearing a single discharge tube; zoospores posteriorly uniflagellate; resting spore thick-walled, formed in a segment of the thallus.

In fresh-water green algae and eelworms.

The genus has been rejected by Fischer (1892), Minden (1915), and others, being considered by them to be based on two-celled forms of *Myzocytium*. Scherffel (1926a:213), however, points out that, in contrast to *Myzocytium*, uniflagellate zoospores are formed in *Bicricium*. He further implies that in the formation of the resting spore no sexuality is involved, since one of the two thalli opens to the outside and probably is a sporangium. If the fungus were a species of *Myzocytium* this thallus would ordinarily function as an antheridium. The argument is weakened here, however, by the fact (not mentioned by Scherffel) that the "oögonium" also possesses an open tube (Sorokin, *op. cit.*, fig. 46).

The proper disposition of the genus is still a matter of doubt. Enough is known about it, however, to place it in the Achlyogotonaceae near *Achlyogenet* and *Septolpidium*.

¹ See also Sorokin, *Revue Mycologique*, 11: 138. 1889.

BICRICIUM LETHALE Sorokin

Arch. Bot. Nord France, 2:37, fig. 45. 1883 (separate)¹
 (Figure 8 J, p. 130)

Sporangia irregularly narrowly ellipsoidal, strongly constricted at the thin cross wall which separates them, each of the free ends provided with a single fairly long gradually tapering tube, the tip of which penetrates the wall of the substratum; zoospores narrowly ovoid, with a strongly acuminate apex and a small basal colorless globule, uniflagellate, emerging through the open end of the discharge tube; resting spore not observed.

In dead eelworms, EUROPEAN RUSSIA, ASIATIC RUSSIA.

IMPERFECTLY KNOWN SPECIES OF BICRICIUM

? BICRICIUM NASO Sorokin

Arch. Bot. Nord France, 2:37, fig. 47. 1883 (separate)²

Sporangia narrowly ovoid, one in each semicell of the alga, the narrower end terminating in a distinct swelling which gives rise to a long discharge tube penetrating the wall of the substratum and elongating for a considerable distance outside, the isthmus joining the two sporangia consisting of a long narrow tube; all other characters unknown.

In *Arthrodeshmus* sp., ASIATIC RUSSIA.

Sorokin suggests that the parasites of desmids figured by Reinsch (1878: pl. 17, figs. 6, 11-12) might better be placed in *Bicricium* than in *Myzocytium*, where Cornu (1877b:228) said they belonged. A comparison of Reinsch's figures with those of *Myzocytium* by Zopf (1884: pl. 14), leaves little doubt as to the correctness of Cornu's contention. It is probable that the present species of *Bicricium*, with its discharge tube bearing a bulbous endobiotic base, also belongs in *Myzocytium*, since it has a very different aspect from the other species.

¹ See also Sorokin, *Revue Mycologique*, 11:138, pl. 83, figs. 72-74. 1889.

² See also *ibid.*, pl. 81, fig. 117. 1889.

? *BICRICIUM TRANSVERSUM* Sorokin

Arch. Bot. Nord France, 2:37, fig. 46. 1883 (separate)¹

(Figure 8 I, p. 130)

Sporangium narrowly ellipsoidal, with a narrow discharge tube; zoospores not observed; adjacent cell subspherical, bearing a spherical thick-walled resting spore, method of formation and germination unknown.

In filaments of *Cladophora* sp., ASIATIC RUSSIA.

SYNCHYTRIACEAE

Thallus endobiotic, holocarpic, without a specialized vegetative system, at maturity converted either into a sorus of inoperculate sporangia, a prosorus, or a resting spore; sporangia formed endo- or epibiotically, always at first surrounded by a common soral membrane; zoospores posteriorly uniflagellate, with a single globule; sexual reproduction, where known, by conjugation of isogamous planogametes, the zygote forming the thick-walled endobiotic resting spore, which upon germination functions either as a sporangium or a prosorus.

The largest genus of the family, *Synchytrium*, is composed of species all of which are obligate parasites of flowering plants (Tobler, 1913). Many of these, as, for example, *S. endobioticum*, the cause of the black-wart disease of Irish potatoes, attack hosts of great economic importance. The genera *Micromyces* and *Micromycopsis* are parasitic on green algae and have thus far been observed only on members of the Conjugatae.

Well-authenticated occurrences of sexuality have been observed only in *Synchytrium* (Curtis, 1921; Kusano, 1930a), although Couch (1931:231) presents evidence that the resting spore of *Micromyces* may possibly be formed from a zygote.

¹ See also Sorokin, *Revue Mycologique*, 11:138, pl. 78, fig. 76. 1889.

KEY TO THE GENERA OF THE SYNCHYTRIACEAE

- [Parasitic on flowering plants; thallus large, forming a sorus, prosorus, or resting spore; zoospores freed outside the host cell *SYNCHYTRIUM*¹]
 Parasitic on algae; thallus small, always forming a prosorus or a resting spore; zoospores freed inside or outside the host cell
 Sorus formed endobiotically, released directly through an aperture in the wall of the prosorus; zoospores freed inside the host cell *MICROMYCES*, p. 136
 Sorus formed epibiotically at the tip of a discharge tube; zoospores freed outside the host cell *MICROMYCOPSIS*, p. 140

MICROMYCES DANGEARD

Le Botaniste, 1:55. 1889

(Figure 9 A-C, p. 138)

Thallus at first naked, somewhat amoeboid, later walled, endobiotic, holocarpic, without a specialized vegetative system, forming the rudiment of the prosorus or resting spore; prosorus thick-walled, spiny; sorus endobiotic, thin-walled, smooth, attached to the prosorus, forming endobiotically from four to twenty-four or more inoperculate uni- or multiporous angular sporangia; zoospores minute, posteriorly uniflagellate, with one or two globules; resting spore thick-walled, spiny, upon germination functioning as a prosorus.

Parasites of fresh-water green algae and, so far as is known, occurring only in members of the Conjugatae.

Before their fungous nature was understood the spiny prosori and resting spores were referred to by algologists as "asterospheres."

In all species the sporangia are liberated upon the bursting of the common soral membrane.

KEY TO THE SPECIES OF MICROMYCES

Spines of prosorus 4-7.5 μ long

Zoospores about 1 μ long *M. Zygogonii*, p. 137

Zoospores 6 μ long by 2 μ thick *M. Petersenii*, p. 139

Spines of prosorus 10-33.6 μ long *M. longispinosus*, p. 139

¹ Not treated here; see Tobler (1913).

MICROMYCES ZYGOGONII Dangeard

Le Botaniste, 1:52, pl. 2, figs. 1-10. 1889

(Figure 9 C, p. 138)

Prosorus spherical, 11-18 μ in diameter, with a thickened colorless wall the outer surface of which is covered with numerous slender sharp tapering spines 4-7.5 μ long; sorus emerging through a small pore formed in the wall of the prosorus, at first spherical, 13-25 μ in diameter, with a thin wall, at maturity becoming somewhat angular owing to the formation of from four to eight pyramidal truncate sporangia with rounded bases, sporangia 6-11 μ broad by 12 μ high, with from one to three small discharge papillae; zoospores spherical, ovoid or fusiform, 1-2 μ long, with a minute colorless refractive globule and a fairly long flagellum, movement hopping or amoeboid; resting spore spherical, about 12.5 μ in diameter, covered with somewhat shorter spines than those on the sporangium, inner wall thick, brownish or brownish red, germination not observed.

Parasitic in various Conjugatae and often causing pronounced swelling and elongation of the host cell. In *Zygomonium sp.*, Dangeard (*loc. cit.*; 1890-91c:245, pl. 17, figs. 2-8), *Spirogyra quadrata*, Denis (1926:14, fig. I, 2), FRANCE; *Zygomonium sp.*, de Wildeman (1891:172), BELGIUM; *Mougeotia sp.*, Petersen (1910:556, fig. 27c), DENMARK; Conjugatae, Pringsheim (1895), Minden (1915:281), *Netrium sp.*, *Mougeotia sp.*, Schulz (1922: fig. 91; 1923: figs. 10-11), *M. scalaris*, Heidt (1937:204, figs. 1-8), GERMANY; *Mougeotia sp.*, Huber-Pestalozzi (1931:88, pl. 3, figs. 1-23), SWITZERLAND; *Mougeotia sp.*, *Zygomonium sp.*, Couch (1937:595, figs. 1-8), *Mougeotia sp.*, Sparrow (MICHIGAN), UNITED STATES.

Huber-Pestalozzi (*loc. cit.*) and Heidt (*loc. cit.*) give references to the older algological literature containing descriptions of "asterospheres." (See also Thwaites, 1846-47; Shadbolt, 1852; Smith, 1853; de Bary, 1858; Reinsch, 1879; Pringsheim, 1895.)

De Wildeman (1900a:1) has given the name *Micromyces Mesocarpi* to a species which differs from the present one in not causing hypertrophy of the algal cell and in forming the sorus at the tip of a narrow canal on the outside of the host. He was no doubt dealing with a species of *Micromycopsis*.

The presence of distinct hypertrophy in infected cells has been

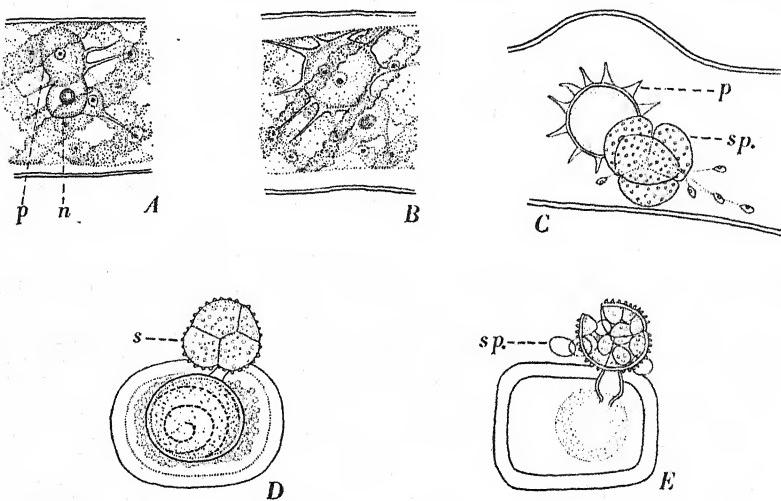


FIG. 9. Synchytriaceae

A-B. Micromyces longispinosus Couch ($\times 417$) in *Spirogyra*: *A*, portion of cell of *Spirogyra* with two young thalli (*p*) attached to host nucleus (*n*); *B*, nearly mature spiny thallus attached to host nucleus. *C. Micromyces Zygogonii* Dangeard ($\times 740$), part of empty *Mougeotia* cell with discharged spiny prosorus (*p*) and four sporangia (*sp.*); uppermost sporangium is discharging its zoospores. *D-E. Micromyopsis cristata* Scherffel ($\times 500$) in *Hyalotheca*: *D*, empty endobiotic resting spore seen from top, with tube and epibiotic rough-walled sori (*s*) of sporangia to which it has given rise; spiral arrangement of spines on resting spore is clearly seen; *E*, smooth-walled endobiotic resting spore and, connected to it by a tube, the ruptured sorus, within which are undischarged sporangia; several empty sporangia (*sp.*) have fallen away from the group.

(*A-B*, Couch, 1931; *D-E*, Scherffel, 1926a)

noted by all observers of *Micromyces Zygogonii*, as has also the attraction of the young thallus for the host nucleus rather than for the chloroplast. The infected cell may become from two to three times longer and wider than healthy cells. Lateral expansion is often accompanied in its later stages by a strong bulging out of the side wall. This wall may fracture at its apex and allow for the passage of the undigested contents of the alga. If disintegration of the algal wall does not take place elsewhere the same orifice undoubtedly also allows the zoospores access to the outside medium. Heidt,

who maintained infected algae for months in 1 per cent agar, observed that the parasite could cause elongation not only of the whole cell but also of a part of the cell and that the same parasite might in one culture bring about complete disintegration of the cell and in another only slightly affect its vitality. Attempts to infect Conjugatae with the fungus appear to have been uniformly unsuccessful.

Cytological observations by Dangeard (1890-91c) showed that the prosorus was uninucleate and that after formation of the sorus active nuclear division occurred, accompanied by a distinct decrease in nuclear size.

MICROMYCES PETERSENII Scherffel

Arch. Protistenk., 54:209, pl. 10, figs. 78-79. 1926

Prosorus spherical, with sparingly dispersed short conical spines covering the outer surface; sorus as in *Micromyces Zygogonii*; zoospores narrowly spindle-shaped, 6μ long by 2μ thick, with a large laterally placed strongly refractive colorless oil globule and a long extremely delicate posterior flagellum, movement somewhat amoeboid.

In *Mougeotia sp.*, HUNGARY.

Scherffel considers that the species is distinct from *Micromyces Zygogonii* on the basis of differences in host plant and character of the spines and especially in the large ($6 \times 2 \mu$) fusiform rather than spherical (1μ in diameter) zoospores. Primarily because of these large zoospores it is maintained here as a separate species.

MICROMYCES LONGISPINOSUS Couch

Mycologia, 29:592, figs. 9-14. 1937

(Figure 9 A-B)

Prosorus more or less spherical, $10-33.6 \mu$ in diameter (mostly 21μ), outer wall irregularly reticulate, bearing from twelve to twenty-four straight or somewhat curved hyaline tapering spines up to 22μ long (mostly about 12μ), sorus smooth-walled, spherical or ovoid; sporangia from eight to twenty-four or more, usually polygonal, sometimes pyramidal with rounded base and truncate apex, 8.4μ high by 9.6μ broad; zoospores numerous, subspherical or ovoid, 1μ thick, with one or two globules and a slender flagellum, escaping through a pore formed in the narrow apex; resting spore subspherical,

16–21 μ in diameter, somewhat angular, thick-walled, with long tapering spines, pale yellow brown, upon germination functioning as a prosorus. (Modified from Couch.)

Parasitic in *Spirogyra* sp., UNITED STATES.

As in *Micromyces Zygogonii* the thallus and prosorus are uninucleate (Fig. 9 A–B, p. 138), nuclear division taking place only in the sorus. Couch also presents evidence that the resting spore upon germination is uninucleate. There is some reason for believing that, as in *Synchytrium*, the so-called "zoospores" may behave as planogametes and fuse in pairs, giving rise to a planozygote which presumably penetrates the alga and forms the resting spore. What is known of the cytology of *Micromyces* indicates that it closely resembles *Synchytrium*.

Further observations are needed on the method of infection. Couch (1931) states that the zoospore softens the wall and forms a perforation through which it flows. Whether or not a cyst is left on the surface has evidently not been determined. In view of the small size of the zoospore such a cyst, if formed, would probably be a difficult structure to observe.

IMPERFECTLY KNOWN SPECIES OF MICROMYCES

? MICROMYCES SPIROGYRAE Skvortzow

Arch. Protistenk., 51:433, fig. 6. 1925

Prosorus spherical or ellipsoidal, with a thick wall, the outer surface densely covered with slender rodlike isodiametric spines 3.5–3.8 μ long; sorus, sporangia, and zoospores not observed; resting spore 22.5–26 μ long by 18–22.5 μ wide, with a thick brown wall, densely covered with spines, germination not observed.

In *Spirogyra inflata*, MANCHURIA.

The true affinities of the organism cannot be determined until the zoospores have been observed.

MICROMYCOPSIS SCHERFFEL

Arch. Protistenk., 54:202. 1926

(Figure 9 D–E, p. 138)

Thallus endobiotic, holocarpic, without a specialized vegetative system, at maturity transformed into a thick-walled smooth or spiny

prosorus, the latter producing a tube which pierces the wall of the substratum and through which the contents are discharged; sorus extramatrical, sessile or elevated, somewhat thick-walled, smooth or spiny, formed at the tip of the prosoral tube, from which it is separated by a cross wall, at maturity breaking along definite sutures to liberate the inoperculate thin-walled spherical or ellipsoidal sporangia; zoospores few, posteriorly uniflagellate, with a single globule; resting stage not observed.

In fresh-water Conjugatae.

The genus differs from *Micromyces* in that the prosorus forms a discharge tube, the sorus has a thick-walled membrane, and the small thin-walled somewhat spherical sporangia bear only a few zoospores.

KEY TO THE SPECIES OF MICROMYCOPSIS

- Prosorus and sorus spiny *M. cristata*, p. 141
Prosorus smooth
 Sorus sessile, smooth *M. Fischerii*, p. 142
 Sorus at tip of the prolonged prosoral tube, spiny *M. zygnaemicola*, p. 143

MICROMYCOPSIS CRISTATA Scherffel

Arch. Protistenk., 54:202, pl. 9, figs. 65-68, pl. 10, figs. 69-76. 1926

(Figure 9 D-E, p. 138)

Prosorus spherical and 11-16 μ (mostly 14 μ) in diameter or spheroidal and 13-16 \times 18-20 μ , with a thickened dark-brown wall, the outer surface bearing a helical series of spines making from five to six equidistant turns, occasionally smooth-walled or with irregularly arranged spines, discharge tube cylindrical, clavate, or irregularly curved, never extending beyond the host wall; sorus sessile, spherical, equal in size to the prosorus, wall thickened, deep blackish brown, the outer surface covered uniformly with short blunt spines; soral wall at maturity splitting along three or four planes; sporangia very thin-walled, spherical or by mutual contact somewhat polygonal; zoospores spherical, with a colorless eccentric globule and a long flagellum, from three to five formed in a sporangium, escaping through a pore in the sporangium wall; resting stage not observed.

Parasitic, or perhaps only saprophytic, in *Hyalotheca dubia*, Scherffel (*loc. cit.*), HUNGARY; *Hyalotheca dissiliens*, Cejp (1933a:2, pl. 1, fig. 4), GERMANY.

Scherffel presents evidence that the sporangia may be freed from the soral membrane before maturity of the zoospores, in which case they emerge as relatively large (4μ in diameter) uniflagellate "non-swarming" amoeboid swarmers with a single globule, which encyst and then produce the zoospores endogenously. Typically, however, the true zoospores are formed while the sporangia are within or in the vicinity of the open sorus wall. Scherffel's interpretation of the sporangial nature of the "nonswarming" swarmers is not based upon actual continuous observation but upon stages found in his material. If this sequence of events is confirmed it will have a very important bearing on the homologies of the prosorus, sorus, and sporangia of the Synchytriaceae. Cejp (1932a:2) found only the typical non-flagellate sporangial stage in another species, *Micromycopsis zygnaemicola*.

MICROMYCOPSIS CRISTATA var. MINOR Sparrow, Mycologia, 24:273,
text fig. 1 d-e. 1932

Prosorus bearing a helical series of spines, occasionally smooth-walled, $8.5-10.4 \mu$ (usually 8μ) in diameter; discharge tube narrowly cylindrical, isodiametric; sorus sessile, 7.8μ in diameter, brown, covered with short sharp spines, splitting into three parts; other phases not observed.

In *Spirogyra* sp., UNITED STATES.

The variety differs from *Micromycopsis cristata* in being smaller and in bearing sharp spines on the sorus wall.

MICROMYCOPSIS FISCHERII Scherffel

Arch. Protistenk., 54:208, pl. 10, fig. 77. 1926

Prosorus spherical, with a thick smooth wall, 11μ in diameter, discharge tube more or less long, cylindrical, not extending beyond the surface of the outer wall of the host; sorus spherical, 12μ in diameter, with a thin smooth colorless wall, sessile on host cell, divided by somewhat radially arranged sutures, the whole cut off by a wall from the discharge tube; other characters unknown.

In *Zygomonium*, HUNGARY.

The species differs from *Micromycopsis cristata* in having a

smooth-walled prosorus and in forming more segments (sporangia) in the sorus. Scherffel's figure of *M. Fischerii* bears a close resemblance to his figure of *M. cristata* (Fig. 76).

MICROMYCOPSIS ZYGNAEMICOLA Cejp

Bull. Internat. Acad. Sci. Bohême, 42(3):2, pl. 1, figs. 5-10, pl. 2, figs. 3-4.
1933 (separate)

Prosorus spherical and 10-13 μ in diameter or ellipsoidal and 9-10 \times 12-13 μ , with a thickened smooth wall, discharge tube 3-4 μ in diameter, long; sorus non sessile, borne at the tip of the discharge tube, spherical, 13-15 μ in diameter, with a somewhat thickened brownish wall covered by short blunt spines; soral wall at maturity splitting along three sutures into three tetrahedral portions; sporangia spherical or nearly so, thin-walled; zoospores and resting spore not observed.

Parasitic in *Zygnema stellina*, GERMANY.

PHLYCTIDIACEAE

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic cyst either expanding and becoming an inoperculate sporangium, a prosporangium, or a thick-walled resting spore and the endobiotic part functioning as the vegetative system, or the cyst not enlarging and either evanescent or persistent, in which case the endobiotic part forms the reproductive organ as well as the vegetative system; zoospores posteriorly uniflagellate, generally with a single globule; sexual reproduction, where known, by fusion of aplanogametes borne in thalli; resting spore upon germination functioning as a sporangium or prosporangium.

Primarily parasites and saprophytes of fresh-water algae, microscopic animals, and submerged pollen grains.

The family includes the greater part of the fungi commonly referred to as "chytrids" and corresponds roughly to the "Rhizidiaceae" (excluding *Rhizidium* and its close allies) of most monographers.

A comparison of the methods of development of *Phlyctidium*, *Rhizophydium*, *Phlyctochytrium*, *Rhizidiopsis*, *Scherffeliomyces*, *Corallochytrium*, and perhaps *Entophlyctis*, *Diplophlyctis*, and *Podochytrium*, indicates that they are probably closely related.

KEY TO THE SUBFAMILIES AND GENERA OF THE
PHLYCTIDIACEAE

Sporangium epibiotic or extracellular,¹ resting spore epi- or endobiotic; vegetative system varied in nature; zoospore cyst almost always persistent and functional

Subfamily PHLYCTIDIOIDEAE, p. 146

Body of the encysted zoospore wholly or in part enlarging to form a sporangium, the latter usually sessile, with or without a sterile base

Epibiotic or extracellular part completely fertile; endobiotic part varied

Whole body of the spore enlarging

Endobiotic part a distinctly double-contoured tube, irregular sac, sphere, or papilla, never branched or tapering; zoospores assuming motility at or soon after discharge PHLYCTIDIUM, p. 146

Endobiotic part a single tapering rhizoid or a branching system of rhizoids arising from an apophysis or directly from the tip of the germ tube or a prolongation of it

Endobiotic part a tapering rhizoid or a branching system of rhizoids arising from the tip of the germ tube

Sporangium and resting spore epibiotic; rhizoids developed to a varying degree; parasitic or saprophytic on a variety of substrata

RHIZOPHYDIUM, p. 158

Sporangium extracellular, resting spore endobiotic; rhizoids forming a bushy tuft of small extent; on

Pandorina DANGEARDIA, p. 219

Endobiotic part with the rhizoids arising from an apophysis

¹ I.e. imbedded in material of the host, as, for example, in a gelatinous sheath, but resting on the cytoplasm (*Dangeardia*, etc.).

- Sporangium smooth or ornamented, without an apiculus, the discharge pore usually apical; resting spore epibiotic *PHLYCTOCHYTRIUM*, p. 220
- Sporangium with a spiny wall, smooth apiculus, and lateral discharge pore; resting spore endobiotic *BLYTTIOMYCES*, p. 239
- Only a portion of the spore body enlarging, the remainder appearing as a basal cyst attached to the wall of the sporangium *RHIZIDIOPSIS*, p. 241
- Epibiotic part with a sterile septate base or a small knoblike structure on which the sporangium rests; endobiotic part knoblike or rhizoidal
- Sterile part a small knob on which the sporangium rests; endobiotic part knoblike *PHYSORHIZOPHIDIUM*, p. 242
- Sterile part conspicuous and an integral component or continuation of the base of the fertile portion; endobiotic part rhizoidal *PODOCHYTRIUM*, p. 243
- Body of the encysted zoospore either sessile and enlarging to form a prosporangium or lying free in the water, not enlarging, and producing at the tip of the germ tube an appressorium which expands to form the sporangium; sterile base never formed
- Body of the encysted zoospore sessile, enlarging to form a prosporangium, the endobiotic part consisting of a series of intercommunicating broad lobes *SACCOMYCES*, p. 246
- Body of the encysted zoospore producing at the tip of a germ tube an appressorium which expands to form the sporangium, endobiotic part completely rhizoidal, or apophysate and bearing a distal complex of stubby digitations
- Endobiotic part rhizoidal *SCHERFFELIOMYCES*, p. 247
- Endobiotic part apophysate, with a distal complex of stubby digitations *CORALLIOCHYTRIUM*, p. 249
- Sporangium endobiotic, resting spore endobiotic; vegetative system rhizoidal; zoospore cyst usually evanescent
- Subfamily ENTOPHLYCTOIDEAE, p. 250
- Vegetative part rhizoidal, generally monophagous
- Sporangium spherical, pyriform or irregular, never strongly tubular; typically forming a single discharge tube
- Rhizoids or rhizoidal axes arising directly from the sporangium *ENTOPHYLCTIS*, p. 250
- Rhizoids arising from an apophysis *DIPLOPHLYCTIS*, p. 261

- Sporangium strongly tubular; forming one or more discharge tubes MITOCHYTRIDIUM, p. 266
- Vegetative part an isodiametric coenocytic or septate tube; generally polyphagous
- Vegetative part broadly tubular, nonseptate RHIZOSIPHON, p. 268
- Vegetative part a narrow septate tube APHANISTIS, p. 269

SUBFAM. PHLYCTIDIOIDEAE

Sporangium epibiotic or extracellular, resting spore epi- or endobiotic; vegetative system varied in nature; zoospore cyst usually persistent and functional.

PHLYCTIDIUM (BRAUN) RABENHORST

Flora Europaea algarum, 3:278. 1868 (sensu recent. Serbinow, Scripta Bot. Horti Univ. Imper. Petro., 24:158. 1907)
 (Figure 10 A-B, p. 152)

Chytridium, subgen. *Phlyctidium* Braun, Abhandl. Berlin Akad., 1855:74.
 1856. Non *Phlyctidium* Wallroth, Flora cryptogamica Germaniae,
 2:416. 1833.

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming the rudiment of the sporangium or resting spore, the endobiotic part producing the unbranched, tubular, peglike, clavate, knoblike, or discoid haustorium; sporangium inoperculate, uni- or multiporous; zoospores formed within the sporangium, posteriorly uniflagellate, generally with a single globule; resting spore thick-walled, borne like the sporangium, apparently asexually formed.

Primarily parasites and saprophytes of fresh-water algae.

It is sometimes difficult to determine whether a fungus is a species of *Phlyctidium* or *Rhizophydiuum*. The distinctions given here are no doubt artificial and the genus *Phlyctidium* is not recognized by all investigators (Scherffel, 1926a:186). In practice, however, its separation from *Rhizophydiuum* is highly useful. If the haustorium gives definite evidence of being almost isodiametric or is distally expanded, unbranched throughout, and must be depicted as a double rather than a single line, the fungus is placed in *Phlyctidium*.

Karling (1939a) has suggested the suppression of the name *Phlyctidium*, because of its earlier use by Wallroth (1833) for a genus of

Ascomycetes, and the substitution of a new name, *Tylochytrium*. All species of Wallroth's genus have long since been transferred to other genera and *Phlyctidium* possesses no status among the Ascomycetes. In view of this fact as well as of the long- and well-established use of the name for certain chytridiaceous fungi, *Phlyctidium* should be treated as a *nomen conservandum*.

KEY TO THE SPECIES OF PHLYCTIDIUM

- Endobiotic part (haustorium) uniformly tubular, clavate, or expanded distally
 - Sporangium smooth-walled
 - Sporangium spherical or ellipsoidal, somewhat urceolate after discharge, 16–70 μ in diameter, haustorium a distally expanded peg *P. megastomum*, p. 148
 - Sporangium urceolate, 15–17 μ in diameter, haustorium tubular throughout *P. olla*, p. 149
 - Sporangium wall ornamented
 - Sporangium broadly urceolate or broadly ovoid, with an apical collarette of from four to eight plain prominent teeth
..... *P. Brebissonii*, p. 149
 - Sporangium spherical or slightly ovoid, wall covered with short sharp spines *P. spinulosum*, p. 150
- Endobiotic part spherical, knoblike, discoid, or very short and peg-like
 - Sporangium attached laterally, appearing more or less procumbent
 - Sporangium sessile, irregularly shaped, in general broadly pyriform or ovoid and asymmetrical, strongly arched or reflexed (anatropous), attached laterally near the narrower end *P. anatropum*, p. 150
 - Sporangium elevated on a short stalk, obpyriform
..... *P. Tabellariae*, p. 151
 - Sporangium basally attached, upright, pyriform, ellipsoidal, ovoid, or spherical
 - Sporangium pyriform, occasionally ellipsoidal
 - Haustorium small and knoblike, formed just beneath the sporangium; the latter symmetrically pyriform, with a small papilla *P. Chlorogonii*, p. 151
 - Haustorium spherical, formed at the tip of a slender filament arising from the base of the sporangium; the latter pyriform or ellipsoidal, with a broad blunt apex
..... *P. Eudorinae*, p. 153

Sporangium ovoid or spherical

Haustorium knoblike or discoid

Sporangium spherical, parasitic on *Bumilleria*

P. Bumilleriae, p. 155

Sporangium ovoid or somewhat ellipsoid, parasitic on

sporangia of *Phlyctidium Bumilleriae* *P. anomalum*, p. 155

Haustorium a short blunt peglike tube which projects only

slightly beyond the inner face of the algal wall.

P. brevipes, p. 156

PHLYCTIDIUM MEGASTOMUM, SP. NOV.¹

Sporangium sessile, spherical or ellipsoidal, becoming somewhat urceolate after discharge, 16.3-70 μ in diameter, with a broad apical papilla, wall smooth, colorless, double-contoured, endobiotic part a short distally expanded peg; zoospores at first spherical, later pyriform, with a colorless globule and a long flagellum, 6.5 μ in diameter, enlarging during swarming to 16.3 μ , moving within the sporangium and escaping through a broad apical pore, surrounded by an evanescent layer of slime; resting spore subspherical, 16.3-26 μ in diameter, with a thick brownish outer wall and a thin wavy inner one, endobiotic part like that of the sporangium, germination not observed.

On vegetative cells and heterocysts of *Anabaena Flos-aquae*,
RUSSIA.

This species is based on the fungus described by Raitschenko (*Bull. Jardin Impér. Bot. St. Petersb.*, 2:124, figs. 1-8. 1902) as *Rhizophydis sphaerocarpum*.

The broad orifice of the discharged sporangium characteristically bore remnants of the inner wall around its margin. Examples of internally proliferated sporangia were frequent. New sporangia were formed in this "false proliferation" from a zoospore which had

¹ *Phlyctidium megastomum*, sp. nov.—Sporangium sessile, globosum vel ellipsoideum, post dehiscentiam suburceolatum, 16.3–70 μ diam., in papilla lata apicali desinens; membrana levi hyalina duplice, parte endobiotica simplici apice expansa; zoosporis primum sphaericis denum pyriformibus, globulum hyalinum includentibus et flagello longo praeditis, 6.5 μ diam., in sporangio motilitatem exhibentibus et post dehiscentiam per porum apicalem cito valde expansis 16.3 μ diam.; sporis resistentibus subglobosis, 16.3–26 μ diam., membrana duplice circumdatis, exteriore crassa fuscescente, interior tenui undulosa, parte endobiotica eae sporangii simili; modo germinationis ignoto.

Parasiticum in cellulis vegetativis et heterocystis *Anabaenae Floris-aquae*, RUSSIA.

failed to emerge or from a zoospore which had swum into an empty sporangium. The remarkable increase in size and shape of the zoospore during motility appears to be borne out by the figures, but confirmation of this unique phenomenon is needed.

PHLYCTIDIUM OLLA Sparrow

Mycologia, 25:517, fig. I, 14. 1933

Sporangium sessile, urn-shaped, smooth-walled, $13-15 \mu$ high by $15-17 \mu$ in diameter, with a broad apical papilla; haustorium unbranched, inflated, tubular, about 2μ in diameter by about 12μ long; zoospores emerging through a broad pore after the deliquescence of the papilla, ovoid, 5μ long by 3μ in diameter, posteriorly uniflagellate, with a single globule; resting spore not observed.

Parasitic on *Spirogyra sp.*, UNITED STATES.

In its symmetrical urceolate sporangium this species resembles *Rhizophyidium sphaerocarpum* (Zopf) Fischer. The inflated character of the haustorium, however, distinguishes it as a species of *Phlyctidium*. *P. olla* differs from *P. megastomum* primarily in the smaller size of its sporangium ($15-17 \mu$ in diameter compared with $16-70 \mu$) and in the long tubular rather than short clavate haustorium. If Raitschenko's observations on the extraordinary change in size of the zoospores of his fungus during motility are correct (6.5μ to 16.3μ) a further difference is found, for in *P. olla* they remained $5 \times 3 \mu$. Finally, no "false proliferation" of the sporangium was noted in the present species.

PHLYCTIDIUM BREBISSONII (Dang.), comb. nov.

Chytridium Brebissonii Dangeard, Le Botaniste, 1:59, pl. 3, fig. 17. 1889.

Rhizophyidium Brebissonii (Dang.) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):97. 1892.

Sporangium sessile, broadly urceolate or broadly ovoid, with an apical collarette of from four to eight prominent plain teeth, wall fairly stout, smooth, colorless; rhizoid a broad, nearly isodiametric, apparently unbranched filament; zoospores numerous (one hundred or more), ovoid, 2.7μ in diameter, with a colorless eccentric globule and a long flagellum, emerging in a compact mass through a large apical pore; resting spore not observed.

Parasitic on *Coleochaete scutata* in culture dishes, FRANCE.

It seems probable that if the conspicuous rhizoid were branched in the host cell evidences of this would have been observed by Dangeard. The zoospores are cited as "2 μ 7" (2.7 μ ?) in diameter. Possibly a species of *Rhizophydium*.

PHLYCTIDIUM SPINULOSUM Sparrow

Mycologia, 25:516, fig. I, 2. 1933

Sporangium sessile, spherical or slightly ovoid, colorless, generally about 10 μ in diameter, wall covered with short sharp spines 2 μ high; haustorium a single unbranched slightly inflated tube, 10 μ long by 3 μ in diameter; zoospores (usually about eight) 3 μ in diameter, with a single globule and flagellum, escaping through a subapical pore; resting spore not observed.

Parasitic in *Cladophora* sp., UNITED STATES (rare, occurring with *Phlyctochytrium quadricorne*).

An incompletely known form found by Sparrow (1933c:518, pl. 49, fig. 12) in *Cladophora* sp. has a spherical sporangium about 15 μ in diameter which bears a series of tenuous radiating hairs on the outer surface. The haustorium consists of a stout somewhat irregular unbranched filament 40 μ long by 8 μ in diameter and slightly expanded at the point of contact of the inner wall of the alga. No zoospore discharge was seen. Except for the haustorium the organism resembles an immature specimen of *Phlyctochytrium chaetiferum*.

PHLYCTIDIUM ANATROPUM (Braun) Rabenhorst

Flora Europaea algarum, 3:279. 1868

(Figure 10 A-B, p. 152)

Chytridium anatropum Braun, Flora (N. S.), 14:599. 1856; Monatsber. Berlin Akad., 1856:588.

Sporangium sessile, procumbent or upright, irregular, broadly pyriform, ovoid, asymmetrical, strongly arched or reflexed (anatropous), rarely symmetrical, attached laterally near the narrower end to the algal cell, 5-14 μ wide by 15-33 μ (rarely 50 μ) long, wall thin, smooth, colorless; haustorium very small, rounded or short-

peglike; zoospores elongate, 5μ long by 2μ wide, with a minute, inconspicuous globule and flagellum, discharged through a single pore (rarely two) formed at either of the apices and remaining in a loose cluster at the orifice before creeping away, movement strongly amoeboid, the body forming pronounced pseudopodia, swimming motion not observed; resting spore spherical or ovoid, with a smooth thick faintly brownish wall, 10μ in diameter, contents with globules, haustorium like that of the sporangium, germination not observed.

Parasitic on *Chaetophora elegans*, Braun (*loc. cit.*), *Oscillatoria*, Schenk (1858b:8), GERMANY; *Stigeoclonium sp.*, Sparrow (1933c:516, pl. 49, figs. 4-8), Couch (1935a:170, figs. 56-63), UNITED STATES.

PHLYCTIDIUM TABELLARIAE C. Schröter

Neujahrblatt Naturf. Gesell. Zurich, 99: Anmerk. 3, pl. 1, fig. 48. 1897

Sporangium obpyriform, its long axis oblique or nearly parallel with that of the host, $7-13 \mu$ long by $6-10 \mu$ wide, contents oleaginous and refractive, with a rounded somewhat thick-walled upper part and a blunt thin-walled basal discharge papilla; haustorium $2-4 \mu$ long, consisting so far as is known of a slender extramatrical stalk attached near the discharge papilla, elevating the sporangium above the substratum; other features not observed.

On *Tabellaria fenestrata*, SWITZERLAND.

PHLYCTIDIUM CHLOROGONII Serbinow

Scripta Bot. Horti Univ. Imper. Petro., 24:156, pl. 5,
figs. 11-17. 1907

Phlyctidium acre Serbinow, nom. nud., Dnevnik IX Sezda Rusk. Est. i vz., 1901(10):474.

Rhizophydiump Chlorogonii Jaczewski, Opredelitel gribov.... I.-Fiko-mitsety, p. 38. 1931.

Sporangium sessile, broadly and symmetrically pyriform, with a rather small protruding apical papilla, $6-8 \mu$ in diameter, wall thin, smooth, colorless; haustorium an inconspicuous knoblike structure; zoospores spherical, 1.5μ in diameter, with a small colorless refractive globule and flagellum, emerging individually by means of

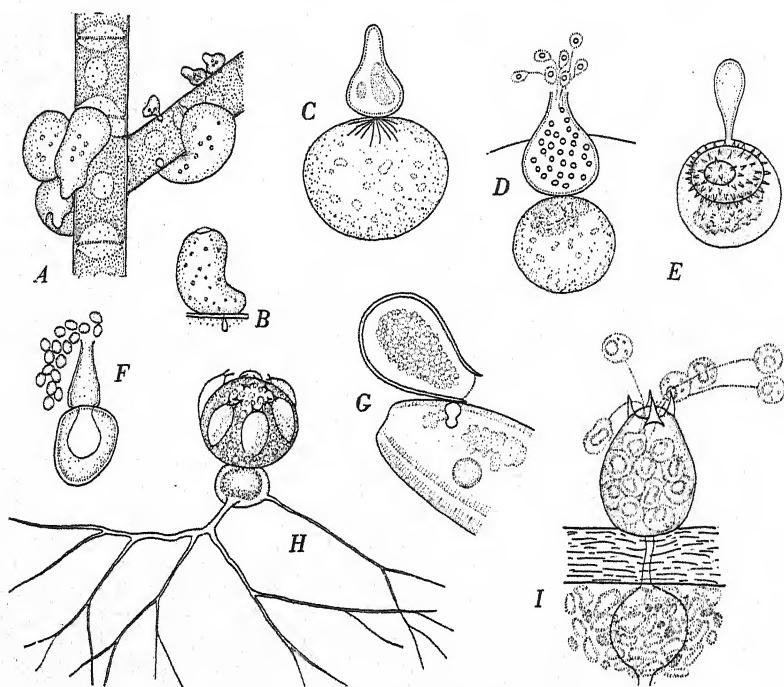


FIG. 10. Phlyctidiaceae

A-B. Phlyctidium anatropum (Braun) Rabenhorst ($\times 690$): *A*, groups of sporangia on *Stigeoclonium*; *B*, single upright sporangium on surface of host. *C-E. Dangeardia mammillata* B. Schröder ($\times 460$) on *Pandorina*: *C*, strongly apiculate sporangium with its bushy rhizoids resting on surface of a cell of a colony; *D*, discharging sporangium with upper part protruding from surface of gelatinous sheath of algal colony; *E*, spiny resting spore within host cell; cyst and infection tube (appendix) are still persistent. *F. Achlyella Flahaultii* Lagerheim, sporangium on surface of *Typha* pollen; zoospores have encysted after discharge from sporangium. *G. Physorhizophidium pachydermum* Scherffel ($\times 620$), sporangium on surface of diatom (*Amphora*?); upper half of knoblike subsporangial structure rests on surface of host; lower half is within it. *H. Phlyctochytrium bullatum* Sparrow ($\times 750$) on *Oedogonium*, epibiotic sporangium ornamented with outer whorl of six bosses and inner whorl of four bifurcated teeth; subsporangial apophysis from which rhizoidal system arises is endobiotic. *I. Phlyctochytrium planicorne* Atkinson ($\times 750$) on *Cladophora*, discharging sporangium ornamented with four plain apical teeth surrounding discharge pore through which zoospores emerge.

(*A-B*, Sparrow, 1938c; *C-E*, Schröder, 1898b; *F*, Lagerheim, 1890; *G*, Scherffel, 1926a; *H-I*, Sparrow, 1938c)

their own motility through a small apical pore; resting spore not observed.

On moribund and dead *Chlorogonium euchlorum*, Serbinow (*loc. cit.*), RUSSIA (?); *Chlorogonium elongatum*, Scourfield (1936:120, pl. 1), ENGLAND.

The species was first mentioned in the minutes of the Ninth Congress of Russian Naturalists and Physicians as *Phlyctidium acre*, but for some reason the name *P. Chlorogonii* was applied to it in the complete description made later (1907) in Russian and German. The size of the zoospore of *P. Chlorogonii* is given as 1–5 μ in the German text, which is obviously a misprint for the 1.5 μ found in the Russian description.

An incompletely observed chytrid with spherical or ellipsoidal sporangia was also shown by Serbinow (1907:158, pl. 4, fig. 37) to possess a small knoblike haustorium like that of *Phlyctidium Chlorogonii*.

PHLYCTIDIUM EUDORINAE Gimesi

Hydrobiologiai Tanulmányok (Hydrobiologische Studien) II. *Phlyctidium Eudorinæ* Gim., n. sp. . . . , pp. 1–5, Németül 6–8, 1 pl., figs. A, 1–8, B, 1–6. Budapest, 1924

Phlyctidium Eudorinæ Skvortzow, Arch. Protistenk., 57:205, fig. 3. 1927.

Rhizophydiump Beauchampi Hovasse, Ann. Protistol., 5:73, figs. 1–4. 1936.

Sporangium imbedded, except for its apex, in the gelatinous sheath of the host colony, generally sessile on the cell of the alga, broadly pyriform or ellipsoidal, with a blunt apex, 10–18 μ high by 4–10 μ wide, wall smooth, colorless, delicate, evanescent; part within the algal contents consisting of a spherical haustorium 1–5 μ in diameter, attached to the base of the sporangium by a slender filament; zoospores 3.5 μ long by 2.6 μ in diameter, escaping upon the rupturing of the apex of the sporangium; resting spore pyriform, thick-walled, 10 μ in diameter, with a large globule in the contents, borne like the sporangium, germination not observed.

Parasitic on *Eudorina* sp., Gimesi (*loc. cit.*), HUNGARY; *Eudorina elegans*, Skvortzow (*loc. cit.*), MANCHURIA; *Eudorina illinoisensis*, Hovasse (*loc. cit.*), FRANCE.

A comparison of the figures and descriptions of the Hungarian and French fungi shows them to be nearly, if not absolutely, identical.

One difference is in the number of zoospores formed, Gimesi stating that from nine to twelve were produced, Hovasse, from twenty to nearly one hundred. Since both accounts were lacking in certain minor but essential points the diagnosis above represents a combination of the two descriptions. Gimesi observed the resting spores, which he said were formed after terminal or lateral copulation of isogamous gametes (see under "Sexual Reproduction," p. 45). Hovasse gives further details on the morphology, development, cytology, and biology of the species. He noted that over 90 per cent of the colonies collected from the pond over a period of ten days were infected by the fungus. The least infected had from one to two chytrids on them, the most, from seventeen to eighteen. Sterility of the colony resulted from heavy infections of the germinocysts. Coenobia bearing numerous chytrid invaders soon dropped to the bottom of the pond and disintegrated.

Concerning the development of the thallus Hovasse observed that the zoospore appears to attack the moving colony, attaching itself on the surface at the point where the flagella emerge. A slender tube is produced from the spore body and passes through the flagellar canal and into the cell contents, expanding distally to form the spherical haustorium. The more proximal portion of the tube and eventually the body of the zoospore itself expand and form the sporangium. The young sporangium is at first terminated by a beaklike process, the body of the zoospore, which disappears later; at maturity the tip of the sporangium is broad. Both Gimesi and Hovasse noted that the young thallus is binucleate.

Hovasse's preparations showed that the single nucleus of the spore migrated from the spore body into the expanding rudiment of the sporangium. There it enlarged and divided, although actual mitotic figures were not observed. The subsequent divisions of the daughter nuclei were not exactly synchronous, one nucleus, for example, being in late anaphase while the other was only in the metaphase. Division was intranuclear, and a centrosome was present at either pole of the spindle. In later stages enlargement of the nuclei occurred, followed by a simultaneous division which reduced their size and changed their configuration. Division of the cytoplasm was preceded by the appearance of large osmophilic vacuoles at one pole of each of the nuclei. Actual cytoplasmic division then

progressed rapidly to all parts of the sporangium and separated the polygonal elements, each of which surrounded a nucleus. These segments became the zoospores.

PHLYCTIDIUM BUMILLERIAE Couch

J. Elisha Mitchell Sci. Soc., 47:256, pl. 17, figs. 66-68. 1932

"Sporangia sessile, globose, $5.4-7.6 \mu$ thick, with a small bulbous or discoid base which extends into the host cell. Spores emerging through an apical pore. Spores not seen. Resting spores not seen" (Couch, *loc. cit.*).

Parasitic on *Bumilleria sp.*, UNITED STATES.

The fungus attacked the healthy cells of the alga and destroyed them. Couch considered the species close to *Phlyctidium Chlorogonii*.

PHLYCTIDIUM ANOMALUM Couch

J. Elisha Mitchell Sci. Soc., 47:256, pl. 17, figs. 69-83. 1932

"Sporangia sessile, ovoid or ellipsoid, $4.2-5.5 \times 7.3-11.7 \mu$, anchored to the host by a very small, bulbous or discoid base. Spore development as in *Rhizophidium globosum*. Spores in sporangium about 1.8μ thick, with a single glistening droplet. Swimming spores not seen. Sporangial discharge through an apical pore. Sporangium collapsing more or less after spore discharge. Resting cells formed from a cell of about the same size and shape as a mature sporangium. The protoplasm collects in the distal half of this cell leaving the proximal half empty and around the protoplasm a rather thick wall is formed. Resting cell with 1-3 oil globules. Rarely the mature resting cell may occupy the entire 'parent' cell being elliptical in shape" (Couch, *loc. cit.*).

Hyperparasitic on sporangia of *Phlyctidium Bumilleriae*, UNITED STATES.

In this curious instance of hyperparasitism of one chytrid by another Couch noted that none of the infected sporangia of the host ever reached maturity. The peculiar two-celled resting body resembles in its method of formation the development of that of *Nephrochytrium stellatum*.

PHLYCTIDIUM BREVIPES (Atkinson) Minden

Kryptogamenfl. Mark Brandenburg, 5:313. 1911 (1915)

Rhizophydiumprevipes Atkinson, Bot. Gaz., 48:322, fig. 2. 1909.

Sporangium sessile, ovoid or spherical, 10.2-24 μ in diameter, with a protruding apical papilla, wall smooth, colorless, double-contoured; haustorium consisting of a short blunt peglike tube which projects only slightly beyond the inner face of the algal wall; zoospores ovoid, about 3 μ in diameter, with a colorless globule and flagellum, escaping through an apical pore about 4 μ in diameter formed upon the deliquescence of the papilla; resting spore not observed.

On gametangia of *Spirogyra varians*, Atkinson (*loc. cit.*), UNITED STATES; vegetative cells of *Oedogonium sp.*, *Spirogyra sp.*, Tokunaga (1934b:388, pl. 11, figs. 1-2), JAPAN.

Atkinson observed that several zoospores which at maturity were unable to escape formed long germ tubes that penetrated the wall of the sporangium. Not having reached a suitable substratum by this means, they quitted their cysts, swarmed again, came to rest, and once more penetrated the sporangium wall with their germ tubes. Atkinson saw in the production of this long germ tube a method whereby the zoospore might without swimming be able eventually to reach a favorable substratum.

IMPERFECTLY KNOWN SPECIES OF PHLYCTIDIUM

? PHLYCTIDIUM DANGEARDII Serbinow

Scripta Bot. Horti Univ. Imper. Petro., 24:163, pl. 6,
figs. 22 A-C. 1907*Rhizophydiumpangeardii* Jaczewski, Opredelitel gribov.... I. Fikomitsety, p. 38. 1931.

Sporangium sessile on the prosporangium of the host, spherical or ovoid, wall smooth, colorless, two-layered, with a single small protruding apical papilla; haustorium not observed; zoospores ovoid, with a small globule and flagellum, about 1.5 μ long, escaping through a small sessile apical pore; resting spore borne like the sporangium, spherical, thick-walled, the inner wall smooth, the outer irregularly undulate, germination not observed.

Parasitic on prosporangia of the chytrid *Saccommyses*, RUSSIA.

No rhizoid is figured by Serbinow. It is possible that the fungus, although placed in *Phlyctidium*, is in reality a *Rozella* parasitic in the sporangium, rather than the prosporangium, of the host.

? *PHLYCTIDIUM MINIMUM* Schroeter

Kryptogamenfl. Schlesien, 3(1):191. 1885

Rhizophyllum minimum (Schroeter) Fischer, Rabenhorst. Kryptogamen-
Fl., 1(4):105. 1892.

Sporangia sessile, spherical, mostly of the same size, about 6μ in diameter, with a short spherical haustorium.

On *Mesocarpus pleurocarpus*, GERMANY.

Fischer believes this may possibly be only the immature stage of *Chytridium Mesocarpi* Fisch. It was not mentioned by Schroeter (1893) when *Phlyctochytrium* was segregated from *Rhizophyllum*, although from its haustorium it may belong in that genus.

Couch (1932:252) has identified a fungus on *Bumilleria* with this species (see *Rhizophyllum sp.*, p. 213).

? *PHLYCTIDIUM SP.* Serbinow

Scripta Bot. Horti Univ. Imper. Petro., 24:158, pl. 4, fig. 37. 1907

Rhizophyllum Serbinovii Jacewski, Opredelitel gribov. . . I. Fikomitsety, p. 38. 1931.

Sporangium at first spherical, then ovoid, with a simple unbranched expanded rounded haustorium, which penetrates only to the second membrane of the "Gloeocystis" stage.

In *Gloeocystis* stage of *Euglena*, RUSSIA.

? *PHLYCTIDIUM SP.* Sparrow

Mycologia, 25:518, pl. 49, fig. 12. 1933

Sporangium spherical, about 15μ in diameter, the wall covered by a series of tenuous, radiating hairs; haustorium a stout (40μ long by 8μ in diameter) somewhat irregular unbranched filament slightly swollen at the point of contact with the inner wall of the substratum; other characters unknown.

On *Cladophora*, UNITED STATES.

RHIZOPHYDIUM SCHENK

Verhandl. Phys.-Med. Gesell. Würzburg, A. F., 8:245. 1858

(Figure 11, p. 164)

Chytridium subgen. *Sphaerostylidium* Braun, Abhandl. Berlin Acad., 1855:75. 1856.

Rhizophyton Zopf, Nova Acta Acad. Leop.-Carol., 52 (7):343. 1888.

Thallus epi- and endobiotic, monocentric, eucarpic, generally monophagous; the epibiotic part forming the rudiment of the sporangium or resting spore, the endobiotic, the branched (rarely unbranched) rhizoidal system; sporangium inoperculate, sessile, uni- or multiporous; zoospores formed within the sporangium, posteriorly uniflagellate, generally with a single globule; resting spore thick-walled, contents with one or more globules, borne like the sporangium, asexually formed or sexually after receiving the contents of a small adnate contributing thallus which persists as a cyst, upon germination functioning as a sporangium or prosporangium.

Primarily parasites and saprophytes of fresh-water algae, plant spores, and microscopic animals.

This is the largest and most complex genus of the chytrids, one in which extensive morphological studies and cross-inoculation work will be necessary before the limits of the species can be established. One species, *Rhizophydiwm graminis* Ledingham (1936), has been found to be parasitic on roots of wheat; another, *R. fungicola* Zimmerman (1902), on hyphae of *Gloeosporium*. *Mastigochytrium Sacchariae* Lagerheim (1892), which is parasitic on perithecia of *Saccharidium Durantae*, may possibly be referable to *Rhizophydiwm*.

It is well realized that the present treatment of this most difficult genus is far from adequate. Characters which appear from the original description of a species to be fixed, well marked, and distinctive are usually found upon careful investigation of a large number of individuals to be subject to wide variation. Thus the number of discharge pores, the size and shape of the sporangium, the extent of the rhizoidal system, the nature of the substratum, and the like, do not always prove constant or decisive. It is easy to appreciate, therefore, how much reliance can be placed on an analytical key such as that on pages 159-162 for the identification of a species of the genus. The whole complex of "species" should be studied, the original papers consulted, and the figures compared.

Those species with a tapering unbranched rhizoid have been placed in *Rhizophydium* rather than in *Phlyctidium*, where at first sight they might seem to belong.

The treatment of such collective species as *Rhizophydium globosum*, *R. sphaerocarpum*, and so on, has been a subject for much deliberation. There has been no attempt to solve with finality the many problems associated with them. An effort has been made, however, to adhere to the original conception of these species as much as possible. This has left some well-described forms without names. It is hoped that further study will show either that they are worthy of specific rank or that they should be placed under an already described species.

KEY TO THE SPECIES OF RHIZOPHYDIUM

- Sporangia predominantly spherical, subspherical, or ovoid, or occasionally broadly obpyriform and upright SECTION I, p. 162
In fresh-water or inland salt pools
Sporangium wall smooth
Discharge pores variable in number and position, sessile or only slightly elevated
Sporangia predominantly spherical or subspherical
Globule of zoospore small (less than half the diameter of the spore body)
Sporangium wall persistent after discharge; on various types of substrata
Typical sporangia large; zoospores numerous
On green algae
Rhizoidal axis not inflated and haustorial; rhizoids extensive
Resting-spore wall covered with minute spines; primarily on desmids
R. globosum, p. 162
Resting-spore wall smooth or somewhat undulate, bearing a small male cell; on *Spirogyra* *R. Couchii*, p. 167
Rhizoidal axis inflated, forming a peglike haustorium; rhizoids short, scarcely visible *R. laterale*, p. 169
On blue-green algae
Rhizoids delicate, inconspicuous
R. subangulosum, p. 170
Rhizoids coarse, conspicuous *R. megarrhizum*, p. 171

- On reproductive organs of *Pythium* *R. Pythii*, p. 172
- On spores of higher plants *R. sphaerotheca*, p. 173
- On cysts of *Vampyrella* *R. Vampyrellae*, p. 174
- Typical sporangia small (6–8 μ in diameter);
zoospores few (from four to six)
R. Constantineani, p. 174
- Sporangium wall deliquescent after discharge; on
diatoms *R. Cyclotellae*, p. 175
- Globule of zoospore more than half the diameter of
the body of the zoospore *R. macrosporum*, p. 175
- Sporangia predominantly ovoid or somewhat citriform
Papilla obliquely placed; primarily on *Tribonema*
R. asymmetricum, p. 176
- Papilla terminal; primarily on green algae
R. mammillatum, p. 177
- Discharge pores one or two, terminating very distinct dis-
charge tubes
Discharge tube single, apical *R. ampullaceum*, p. 178
- Discharge tubes two, opposed (occasionally one)
Tubes narrow, hornlike; rhizoids branched
R. rostellatum, p. 179
- Tubes broad, giving the sporangium a triangular ap-
pearance; rhizoids unbranched ... *R. Haynaldii*, p. 179
- Sporangium wall ornamented with long delicate hairs
R. chaetiferum, p. 180
- In marine waters; on *Codium* *R. codicola*, p. 181
- Sporangia either predominantly spherical at first and urceolate
after discharge, or pyriform SECTION II, p. 181
- Sporangia spherical at first but urceolate (occasionally pyriform)
after discharge
Rhizoids branched
On pollen *R. pollinis-pini*, p. 181
On *Ophiocytium* *R. Sciadii*, p. 184
- Rhizoids little if at all branched
On algae
Sporangia very small (up to 7 μ in diameter); on dia-
toms (*Asterionella*) *R. Schroeteri*, p. 184
- Sporangia larger; on green algae
Sporangia 6–18 μ in diameter by 20 μ high; on vari-
ous green algae, primarily Conjugatae
R. sphaerocarpum, p. 185
- Sporangia 26–50 μ in diameter; on oögonia of *Vaucheria*
R. Vaucheriae, p. 187

- On aquatic Phycomycetes, primarily only the oögonia and oöspores *R. carpophilum*, p. 187
- On nematodes *R. vermicola*, p. 188
- Sporangia pyriform
 - Sporangium wall collapsing and disintegrating immediately after spore discharge
 - Rhizoids unbranched; on *Mischococcus* *R. Mischococci*, p. 189
 - Rhizoids richly branched; on *Chroococcus* *R. agile*, p. 190
 - Sporangium wall persistent after discharge
 - On algae
 - Sporangia smooth-walled
 - Sporangia with an apical discharge pore
 - Primarily on *Chlamydomonas* *R. acuforme*, p. 190
 - On other algae
 - Sporangia small (5–6 μ in diameter); on *Spirogyra*
 - R. minutum*, p. 191
 - Sporangia larger; on various algae
 - Sporangium broadly pyriform, imbedded, save for its apex, in the gelatinous sheath of *Eudorina* *R. Eudorinae*, p. 192
 - Sporangium narrowly pyriform, resting on the outer surface of the substratum; on various algae
 - On the gelatinous sheath of *Apocystis*
 - R. Brauni*, p. 192
 - On the surface of the gelatinous sheath of cysts of *Cryptomonas* or *Pandorina*, or directly on the wall of other algae
 - R. simplex*, p. 193
 - Sporangia with a subapical discharge pore
 - Pore terminating a short discharge tube; sporangium large (16–20 \times 13–18 μ), apiculate, upright; on *Oocystis* *R. pseudodistomum*, p. 194
 - Pore not terminating a tube; sporangia small (7–14 \times 5–9 μ), appearing somewhat tilted; on *Tribonema* *R. granulosporum*, p. 194
 - Sporangia covered with warts *R. verrucosum*, p. 195
 - On eggs of microscopic animals *R. zoophthorum*, p. 195
 - Sporangia predominantly obovoid or obpyriform SECTION III, p. 196
 - Zoospores liberated upon the deliquescence of the upper half of the sporangium wall *R. clinopus*, p. 196
 - Zoospores liberated upon the formation of an apical discharge pore

Discharge pore very broad, its edge reflexed and rimlike; resting spore spiny, without an adherent male cell

R. echinatum, p. 197

Discharge pore smaller, its edge not reflexed; resting spore smooth-walled, resting on a small male cell .. *R. ovatum*, p. 198

Sporangia predominantly citriform or ovoid, or spherical at first but becoming broadly ellipsoidal or fusiform, the long axis of the sporangium parallel with the surface of the substratum

SECTION IV, p. 198

Resting spore spherical or subspherical, without an adherent male cell; on green algae or diatoms

On *Chlamydomonas* and *Gonium* *R. transversum*, p. 198

On diatoms..... *R. irregulare*, p. 199

Resting spore polygonal, with one or two small adherent male cells; on *Tribonema* *R. goniosporum*, p. 200

Sporangia predominantly cylindrical, fusiform, broadly or narrowly ellipsoidal, the long axis at right angles or slightly inclined to that of the substratum SECTION V, p. 201

Sporangia symmetrical, without humplike lobes

Sporangia narrowly ellipsoidal to cylindrical; zoospores pale rose-colored; on *Cladophora* *R. messanense*, p. 201

Sporangia fusiform; zoospores colorless; on diatoms *R. fusus*, p. 202

Sporangia irregularly gibbose, with humplike lobes *R. gibbosum*, p. 203

SECTION I¹

RHIZOPHYDIUM GLOBOSUM (Braun) Rabenhorst

Flora Europaea algarum, 3:280. 1868 (sensu strictu Cohn, Nova Acta Acad. Leop.-Carol., 24:142. 1853)

Chytridium globosum Braun, Monatsber. Berlin Akad., 1855:381; Abhandl. Berlin Akad., 1855:34, pl. 2, figs. 14-18. 1856.

Phlyctidium globosum (Braun) Sorokin, Arch. Bot. Nord. France, 2:19, fig. 12. 1883 (separate).

¹ See also the following imperfectly known species of *Rhizophydium*:

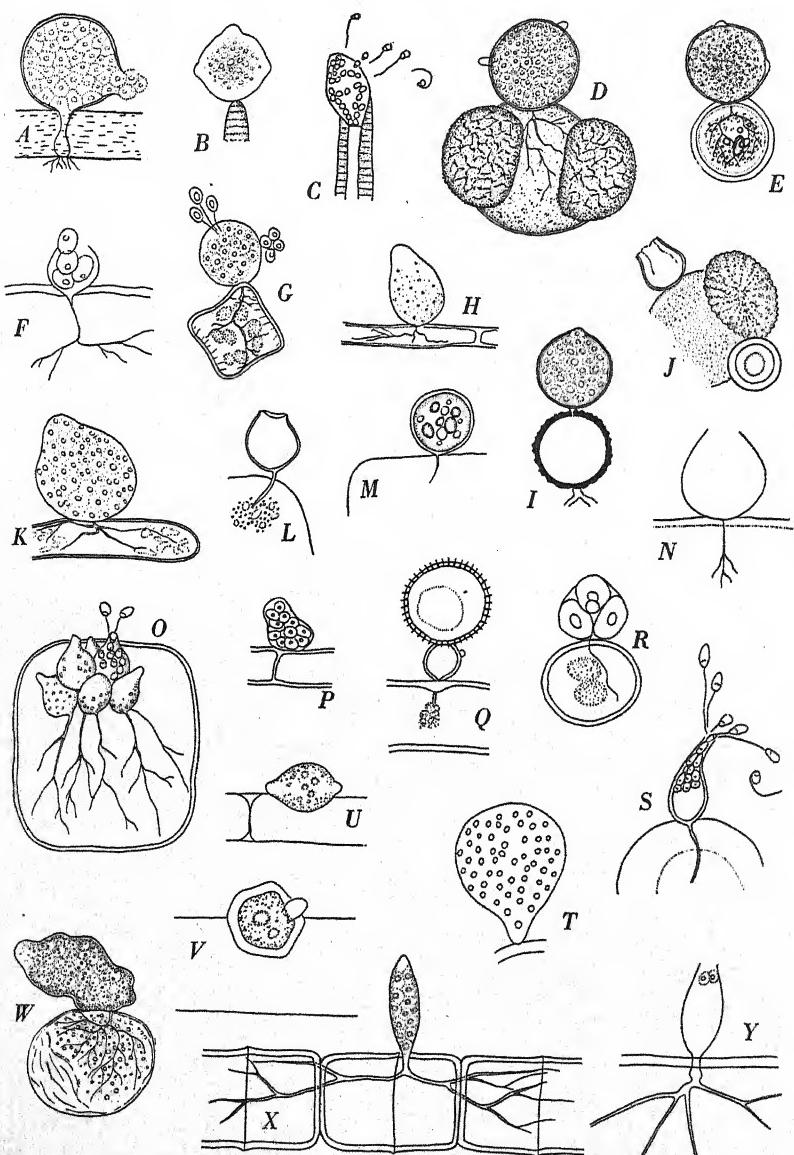
| | |
|----------------------------------|---------------------------------|
| <i>R. caudatum</i> , p. 203 | <i>R. Hyalothecae</i> , p. 207 |
| <i>R. Chrysopyxidis</i> , p. 211 | <i>R. marinum</i> , p. 210 |
| <i>R. decipiens</i> , p. 204 | <i>R. v. Mindeni</i> , p. 207 |
| <i>R. digitatum</i> , p. 205 | <i>R. multiporum</i> , p. 207 |
| <i>R. discinctum</i> , p. 209 | <i>R. Oedogonii</i> , p. 208 |
| <i>R. dubium</i> , p. 205 | <i>R. parasitans</i> , p. 210 |
| <i>R. Epithemiae</i> , p. 206 | <i>R. sporocotonum</i> , p. 208 |
| <i>R. fallax</i> , p. 206 | <i>R. Tranzschelii</i> , p. 211 |
| <i>R. gelatinosum</i> , p. 209 | |

Sporangium sessile, completely spherical, 12–50 μ in diameter or over, wall double-contoured, smooth, colorless, with from two to four protruding discharge papillae on the upper half; rhizoidal system branched, fairly extensive, arising from a short stalk or directly from the tip of the penetration tube; zoospores very numerous, somewhat ellipsoidal, 2–3 μ in diameter, with a flagellum about 20 μ long, escaping individually through one apical pore or through from two to four sessile or slightly elevated pores on the upper half of the sporangium and swimming immediately away; resting spore sessile, spherical, 25–30 μ in diameter, with a thick brownish wall, outer surface covered with small spines, germination not observed.

Parasitic on *Closterium sp.*, causing an epidemic in culture dishes, *Navicula sp.*, (?) *Sphaeroplea annulina*, Cohn (*loc. cit.*, pl. 16, figs. 10–20), (?) vegetative cells of *Oedogonium rivulare*, (?) *Melosira varians*, (?) *Eunotia Amphioxys*, Braun (*loc. cit.*), germlings of *O. tumidulum*, Kloss (in Braun, 1856b:587), *Closterium Lunula*, *Penium digitus*, *Pinnularia viridis*, Schroeter (?) (1885:191), *Pleurotaenium Trabecula*, *Closterium sp.*, *Staurastrum sp.*, Cepp (1933a:3, pl. 1, figs. 5–8, pl. 2, fig. 1), GERMANY; *Closterium spp.*, diatoms, Danegard (1886a:295), FRANCE; *Penium digitus*, *Pleurotaenium Trabecula*, *Genicularia sp.*, *Spirotaenia sp.*, Serbinow (1907:160, pl. 5, figs. 1–3), FINLAND; *Spirogyra sp.*, Atkinson (1894:503; 1909a:321, figs. 1 a–d), UNITED STATES; germling of *Oedogonium sp.*, Scherffel (1926a:230, pl. 10, figs. 116–117), HUNGARY; *Ulothrix sp.*, W. R. I. Cook (1932a:136, figs. 13–19), ENGLAND; *Spirogyra sp.*, Tokunaga (1934b:390, pl. 11, fig. 5), JAPAN.

Though spherical sporangia of this species were observed by Braun on several hosts it was Cohn who reported the nonsexual reproduction and the branched rhizoids. Braun identified the sporangial part of Cohn's fungus with his own, but declared that the rhizoids probably belonged to another organism! Cohn also observed the penetration of the germ tube of the zoospore and the formation of the rhizoids within the alga. Later, however, he declared the same species on *Sphaeroplea* to be without rhizoids.

The species is a difficult one to delimit and, as Fischer (1892:91) aptly pointed out, is either a widespread omnivorous organism or is a collective species in need of further investigation. No sound limitations can be established for it until the morphological variations which occur on different substrata in strains derived from single spores are studied. In the preceding diagnosis an attempt was made

FIG. 11. *Rhizophydiaceae*

to stay within the confines of Cohn's species. The resting-spore stage is that described by Serbinow. No forms were included which did not fall within these limits. Mere records, as well as globose

Explanation of Figure 11

A. Rhizophydi um laterale (Braun) Rabenhorst on *Ulothrix*, sporangium discharging zoospores. *B. Rhizophydi um subangulosum* (Braun) Rabenhorst ($\times 400$), sporangium with discharge papillae, resting on tip of filament of *Oscillatoria*. *C. Rhizophydi um megarryhizum*, sp. nov. ($\times 435$), on *Lyngbia*, discharging sporangium with its broad undulating rhizoid. *D-E. Rhizophydi um sphaerotheca* Zopf: *D*, mature sporangium ($\times 350$) with protruding discharge papillae, on pine pollen; *E*, sporangium ($\times 345$) with two discharge papillae, on microspore of *Isoetes*. *F. Rhizophydi um Constantineani* Saccardo on *Vaucheria*, sporangium discharging its few zoospores. *G. Rhizophydi um Cyclotellae* Zopf ($\times 690$) on *Cyclotella*, sporangium discharging its zoospores through two pores. *H. Rhizophydi um asymmetricum* (Dang.) Minden on *Tribonema*, mature sporangium. *I. Rhizophydi um* sp., germination of resting spore by formation of sporangium. *J. Rhizophydi um pollinispini* (Braun) Zopf ($\times 400$) on pine pollen, empty pyriform sporangium above at left, resting spore below; rhizoidal system not shown. *K. Rhizophydi um Sciadii* (Zopf) Fischer ($\times 690$) on *Ophiocytium*, mature sporangium. *L-M. Rhizophydi um sphaerocarpum* (Zopf) Fischer ($\times 720$) on *Spirogyra* and *Mougeotia*: *L*, empty sporangium; *M*, resting spore. *N. Rhizophydi um vermicola*, sp. nov. ($\times 600$), on nematode, empty sporangium. *O. Rhizophydi um zoophthorum* (Dang.) Fischer on rotifer, group of sporangia on carapace. *P-Q. Rhizophydi um granulosporum* Scherffel on *Tribonema*: *P*, mature sporangium ($\times 540$); *Q*, spiny resting spore on smooth-walled basal male cell ($\times 1500$). *R. Rhizophydi um Mischococci* Scherffel ($\times 1500$) on *Mischococcus*, mature sporangium. *S. Rhizophydi um simplex* (Dang.) Fischer on cyst of *Cryptomonas*, discharging sporangium. *T. Rhizophydi um clinopus* Scherffel ($\times 900$) on diatoms, sporangium. *U-V. Rhizophydi um goniosporum* Scherffel ($\times 1100$) on *Tribonema*: *U*, sporangium with opposed discharge papillae; *V*, angular resting spore with adherent male cell. *W. Rhizophydi um gibbosum* (Zopf) Fischer ($\times 175$) on rotifer egg, maturing sporangium. *X. Rhizophydi um fusus* (Zopf) Fischer ($\times 670$) on *Melosira*, mature sporangium. *Y. Rhizophydi um messanense* Morini on *Cladophora*, sporangium.

(*A*, Karling, 1938e; *B*, Braun, 1856a; *C*, after Dangeard, 1886a; *D-E*, *G, K*, Zopf, 1887; *F*, after Constantineanu, 1901; *H*, after Dangeard, 1890-91c; *I*, Karling, 1939c; *J*, after Braun, 1856a; *L-M*, after Zopf, 1884; *N*, *U-V*, Sparrow, 1936a; *O, S*, Dangeard, 1889b; *P-Q*, Scherffel, 1925b; *R*, Scherffel, 1926a; *T*, Scherffel, 1931; *W*, after Zopf, 1888; *Y*, Morini, 1896)

types which were imperfectly observed, were excluded. The following were considered inadmissible:

1. Schenk (1858a:237), on *Oedogonium sp.* (1858b:8), on *Oscillatoria sp.* and *Anabaena sp.*, GERMANY. No zoospore discharge observed.
2. Sorokin (1883:19, fig. 12), as *Phlyctidium globosum* on diatoms, "Cladophorae," EUROPEAN RUSSIA. No zoospore discharge observed.
3. Dangeard (1888c:142, pl. 5, figs. 16-18), on *Glenodinium*, FRANCE. Probably a new species.
4. Dangeard (1889b:62, pl. 3, fig. 16), on *Vampyrella sp.*, FRANCE. See *Rhizophydiuum Vampyrellae* (Dang.) Minden, page 174.
5. Dangeard (1887a:xxiii; 1889b: pl. 3, figs. 12-13), on *Chlamydomonas*, *Phacotus*, etc., FRANCE. The fungus on *Chlamydomonas* is probably a new species.
6. De Wildeman (1890:20), on *Melosira varians*, BELGIUM. Sporangium spherical, about 16 μ in diameter; escape of the zoospores not observed; appeared to be seven zoospores within the sporangium, each about 5 μ in diameter.
7. De Wildeman (1891:170), on *Hyalotheca sp.*, *Penium sp.*, *Staurastrum sp.*, BELGIUM. Only the sizes of the sporangia are given (12.5-23.5 μ in diameter).
8. De Wildeman (1894:157), on *Melosira sp.*, FRANCE. Record only.
9. H. E. Petersen (1910:552, fig. 24c). Petersen records it on *Penium*, possibly also on other desmids, DENMARK. The substratum of the fungi shown in the figure is not given. From the needle-like unbranched rhizoid, the fungus appears closer to *Phlyctidium*.
10. Schulz (1923:181, fig. 13), on *Pleurotaenium Trabecula*, GERMANY. Sporangium spherical; rhizoids branched; no zoospore discharge observed.
11. Graff (1928:160), on diatoms, UNITED STATES. Sporangium spherical, 25-40 μ in diameter; zoospores escaping through a large terminal opening; rhizoids "similar in development to those of *R. sphaerocarpum* (Zopf) A. Fisch." Probably referable to *Rhizophydiuum sphaerocarpum*.
12. Couch (1932:246). See *Rhizophydiuum Couchii*, sp. nov., page 167. This species also includes the form described by Domján (1936:42), "Type III," and Sparrow (1933c:520).

13. Sparrow (1933c:519), on *Oscillatoria spp.*, *Spirogyra spp.*, *Navicula sp.*, UNITED STATES. Records only. The fungus called *Rhizophydiumpollinis*, described by Sparrow (1932b:275, fig. 2d) on pine pollen in the United States, fits closely the description of *R. globosum*. The resting spores, however, are smooth-walled, a fact inadvertently omitted in the description. See *R. sphaerotheca*, page 173.

14. Sparrow (1936a:441). Three fungi on different substrata, ENGLAND: (1) on rotifer (pl. 19, fig. 19); spherical sporangia 15–20 μ in diameter, ellipsoidal sporangia $43 \times 37 \mu$; zoospores in both types 3 μ in diameter, escaping by from two to three pores; rhizoids stout, well developed; (2) on pollen of *Typha*; sporangium spherical, 12–17 μ in diameter; zoospores 3 μ in diameter, escaping through several pores; rhizoidal system delicate, branched (see *Rhizophydiumpphaerotheca*, p. 173); (3) on *Oscillatoria* (see *R. subangulosum*, p. 170).

15. Sparrow (1936b:258), UNITED STATES: (1) parasitic on *Bryopsis plumosa* (marine); sporangium spherical, 13–18 μ in diameter; rhizoids delicate, branched; zoospores not described; (2) saprophytic on *Rhizosolenia spp.* (marine); sporangium spherical or subspherical, 9–12 μ in diameter; rhizoidal system, so far as observed, consisting of a single delicate unbranched peg; zoospores not observed. The form on *Bryopsis* may possibly be identical with the incompletely known *Rhizophydiumparinum* de Wild. Observations on the zoospore discharge of both these organisms are necessary to place them generically.

Miss Domján (1936) has attempted to divide the fungi she found into types I, II, and III, but the descriptions and figures of these types are too meager to be interpreted.

The descriptions of the following forms designated as *Rhizophydiumpglobosum* have not been examined: Schaarschmidt (1883:62) and Entz, Jr. (1931:12), both based on material from Hungary.

See also *Rhizophydiumpollinis-pini*, page 181.

RHIZOPHYDIUM COUCHII, sp. nov.¹

(Figure 2 G–I, p. 46)

Sporangium sessile, spherical, slightly subspherical, or somewhat ellipsoidal, with from one to three protruding discharge papillae,

¹ *Rhizophydiumpcouchii*, sp. nov.—Sporangium sessile, sphaericum vel subellipsoideum, 11–30 μ diam., papillis 1–3 exsertis praeditum; membrana levi, hyalina, crassissima.

11–30 μ in diameter, wall of variable thickness (up to 2 μ), smooth, colorless; rhizoidal system extensive, much branched, arising from a more or less prolonged, sometimes slightly inflated main axis; zoospores spherical or slightly ovoid, 2–5 μ in diameter, with a small eccentric colorless globule and a long flagellum, escaping slowly, often amoeboidly, through one apical pore or through from two to three apical, subapical, and lateral pores formed upon the deliquescence of the papillae, movement hopping; resting spore spherical or somewhat ellipsoidal, 10–14 μ in diameter, with a thick smooth colorless wall which is occasionally surrounded by an irregular brownish incrustation, contents with a large oil globule, rhizoidal system branched, germination not (?) observed; contributing thallus spherical, thin-walled, 5 μ in diameter, adnate to the receptive plant, sessile, rhizoidal system rudimentary if present.

On *Spirogyra areolata*, *Spirogyra* sp., *Mougeotia* sp., Couch (1932:246, pl. 14), *Spirogyra* sp., Sparrow (1933c:520, pl. 49, figs. 15–22), UNITED STATES.

The species has been described by Couch (*loc. cit.*) under the name *Rhizophydiumpglobosum* and by Sparrow (*loc. cit.*) as *Rhizophydiump* sp. It differs from *R. globosum* in several features, as Couch has pointed out. Most important of these is that the resting spore is smaller (10–14 μ), smooth-walled, and sexually formed (see under "Sexual Reproduction," p. 45). *R. globosum* "Type III" of Domján (1936) is, from the figures, very similar to *R. Couchii*. Since the form is described only in Hungarian a further comparison has not been attempted.

Only one (apical) pore was observed in the sporangia of Sparrow's material, whereas Couch reports one or several in his fungus. This difference is not considered of great significance in view of the strik-

tudine variabili, 2 μ crassa vel tenuiore; parte rhizoidea multiramosa, dispersa, ex trunco interdum vix inflato plus minusve elongato oriente; zoosporis sphaericis vel subovoideis, 2–5 μ diam., lente saepe more Amoebae vel saltuatim transitantibus per poros 1–3 papillarum deliquescentia formatos, vel singulos, apicales vel 2–3 subapicales lateralesque; sporis resistantibus sphaericis vel subellipsoidalibus, 10–14 μ diam., membrana crassa hyalina praeditis et interdum extus incrustatione irregulari fusca vestitis intus globulum oleaceum magnum includentibus; thallo contributario sphaericō, membrana tenui investito, 5 μ diam., ad plantam hospitalem adnato, sessili, cum parte rhizoidal nullā vel rudimentali.

Parasiticum in *Spirogyra* spp., UNITED STATES.

ing similarities which are otherwise apparent in the two fungi. Germination of the resting spores of material which is probably this species has been described by Karling (1939c) (Fig. 11 I, p. 164).

RHIZOPHYDIUM LATERALE (Braun) Rabenhorst

Flora Europaea algarum, 3:281. 1868

(Figure 11 A, p. 164)

Chytridium laterale Braun, Monatsber. Berlin Akad., 1855:382; Abhandl. Berlin Akad., 1855:41, pl. 2, figs. 20-21, 23-26. 1856.

Phlyctidium laterale (Braun) Sorokin, Arch. Bot. Nord France, 2:20, fig. 15. 1883 (separate).

Sporangium sessile, spherical and 9-18 μ in diameter or somewhat ovoid and 10-12 μ in diameter by 12-15 μ high, with from one to three blunt conical subapical lateral or occasionally basal papillae, wall up to 1.7 μ thick, smooth, or occasionally with a basal protrusion, colorless; endobiotic part consisting of a peglike cylindrical or slightly irregular outgrowth, of variable length but usually from two to three times as long as wide, from the tip of which a few delicate rhizoids emerge; zoospores somewhat oblong and 2-2.5 μ long or subspherical and 2.5-3.2 μ in diameter, with a flagellum about 10-15 μ long and an eccentric colorless globule, moving within the sporangium and escaping through from one to three more or less elevated pores 3-5 μ in diameter; resting spore spherical, 12 μ in diameter, colorless or yellowish to amber, with a thick colorless wall which is smooth or bears a hemispherical protrusion, endobiotic part like that of the sporangium, germination not observed.

On *Ulothrix zonata*, Braun (*loc. cit.*), Schenk (1858a:237), GERMANY; *Stigeoclonium*, Sorokin (*loc. cit.*), ASIATIC RUSSIA, EUROPEAN RUSSIA; *Ulothrix zonata*, Serbinow (1907:157, pl. 6, figs. 18-21), EUROPEAN RUSSIA; (?) zygote of *Spirogyra sp.*, Sparrow (1932b:274, fig. 2g), *Ulothrix spp.*, Karling (1938e:pl. 31), UNITED STATES.

Rhizophydiump laterale is one of the two inoperculate species of the Phlyctidiaceae in which Braun observed the endobiotic part. This was a peglike outgrowth which penetrated the wall and rested on the green contents of the alga. At the point of entrance of the fungus the algal wall was swollen, forming what Scherffel (1926a:241) has called a "Schutzhöcker." Karling's fungus differs in two features from Braun's, that is, in the persistence of a part of the cyst of

the zoospore as a hemispherical protrusion, as found in *Chytridium Schenkii* and its allies, and in the possession of rhizoids emerging from the tip of the "peg." Karling considers that the presence of rhizoids shows this fungus to be a *Rhizophydiuum*. Ingold (communication, 1940), however, has found on a thin-walled *Ulothrix* in England a form of this species lacking both rhizoids and hemispherical cyst. There is a possibility that there may be two species involved.

RHIZOPHYDIUM SUBANGULOSUM (Braun) Rabenhorst

Flora Europaea algarum, 3:281. 1868. Non *R. subangulosum* sensu Dangeard, Bull. Soc. Linn. Normandie, III, 9:88. 1884-85,
et auct. recent.

(Figure 11 B, p. 164)

Chytridium subangulosum A. Braun, Monatsber. Berlin Akad., 1855:382;
Abhandl. Berlin Akad., 1855:44, pl. 3, figs. 27-31. 1856.

Sporangium sessile on the apical or other cells of the trichome of the alga, spherical at first but at maturity, upon the formation of from two to three papillae, becoming somewhat angular, 10-25 μ in diameter, wall slightly thickened, smooth, colorless; endobiotic system consisting of a delicate sparingly branched or occasionally unbranched rhizoid; zoospores spherical, 2-2.5 μ in diameter, with a colorless basal globule and a long flagellum, escaping through several pores formed upon the deliquescence of the papillae; resting spore not observed.

On *Oscillatoria tenuis* var. *subfusca*, Braun (*loc. cit.*), (?) germinating spores of *Aspidium*, Schenk (1858b:8), GERMANY; *Oscillatoria* sp., Sparrow (1936a:442, pl. 17, fig. 3), ENGLAND.

As has been previously pointed out (Sparrow, 1936a), this species has apparently been misinterpreted. Braun did not observe the rhizoids (although Rabenhorst [*loc. cit.*] states that they are present), but gave careful figures of the sporangia and zoospores.

The sporangia differ little from those of *Rhizophydiuum laterale* and *R. globosum*. The angular quality becomes evident only when the prominent discharge papillae are formed.

No figures or description are given of Schenk's fungus. Dangeard (1884-85a:88; 1886a:294, pl. 13, figs. 1-5) describes and illustrates a form which differs from Braun's in several important features.

The sporangium is obpyriform or casklike rather than globose, and at maturity it is somewhat angular because of the formation of several papillae. The rhizoid is broad and tubular, unbranched, and extends through a number of cells of the host, becoming somewhat constricted in passing through the transverse cell walls. Subsequent investigators of the chytrids have interpreted Braun's species as modified by Dangeard (de Wildeman, 1890:17, fig. 5; Minden, 1915:323, fig. 14 a-b; Sparrow, 1936a:439, pl. 17, figs. 1-2). It is surprising, as Minden has pointed out, that Braun did not observe the very broad and extensive rhizoid if it was actually present in his material. In view of the fact that it has been shown (Sparrow, *loc. cit.*) that there exists a parasite of *Oscillatoria* with spherical sporangia (angular at maturity) and a very delicate rhizoidal system, it seems more logical to suppose that this was the type observed by Braun, not the form with broad tubular "mycelium." The latter is therefore segregated from *Rhizophydiwm subangulosum* as *R. megarrhizum*, sp. nov. (see below).

Fischer (1892:90) thinks that the fungus found by Schenk on *Aspidium* spores may be referable to *Rhizophydiwm sphaerotheca* rather than to the present species. Although this is probable, there seems to be no reason, other than similarity of substratum, for this conjecture.

RHIZOPHYDIUM MEGARRHIZUM, sp. nov.¹

(Figure 11 C, p. 164)

Chytridium subangulosum, sensu Dangeard, Bull. Soc. Linn. Normandie, III, 9:88. 1884-85.

Sporangium sessile, spherical, broadly ellipsoidal, or obpyriform, with a broad rounded apex, 9-25 μ in diameter, becoming somewhat angular upon the formation of from two to four projecting discharge

¹ *Rhizophydiwm megarrhizum*, sp. nov.—Sporangium sessile, globosum vel late ellipsoidale vel obpyriforme, 9-25 μ diam., apice latum rotundatum, demum subangulosum papillas 2-4 exsertas ferens; membrana levi, hyalina; parte rhizoidea crassa, sparsim ramosa, saepe undulata, polyphaga, 60-65 μ longa vel breviori; zoosporis 10-60 vel numerosis, sphaericis, 2-5 μ diam., globulo basali hyalino et flagello longo praeditis, per poros papillarum deliquescentia formatos extrusis; sporis resistentibus nondum visis.

Parasiticum in *Oscillatoria* et *Lyngbia*, FRANCE.



papillae, wall smooth, colorless; rhizoids broad, sparingly branched, often undulate, polyphagous, up to 60–65 μ or more in length; zoospores from ten to sixty or more, spherical, 2–5 μ in diameter, with a colorless basal globule and a long flagellum, discharged through pores formed upon the deliquescence of the papillae; resting spore not observed.

Parasitic on *Oscillatoria* sp., *Lynghia* sp., Dangeard (1884–85a:88; 1886a:294, pl. 13, figs. 1–5), FRANCE; *Oscillatoria* spp., de Wildeman (1890:17, fig. 5), BELGIUM; *Oscillatoria* sp., Minden (1915:323, fig. 14a–b), GERMANY; *Oscillatoria* sp., Sparrow (1936a:439, pl. 17, figs. 1–2), ENGLAND.

See the discussion under *Rhizophydiwm subangulosum*, page 170. Ordinarily the sporangia are found attached to the apical cells of the trichomes, but Minden says they may be elsewhere, the rhizoid then penetrating only one cell of the alga.

The form shown by de Wildeman has a subsporangial cylindrical prolongation into the host cell; the rhizoid arises from this prolongation. A similar structure is found on an unnamed chytrid inhabitant of *Oscillatoria* figured by Sparrow (1933c:528, fig. I, 21).

RHIZOPHYDIUM PYTHII de Wildeman

Ann. Soc. Belge Micro. (Mém.), 21:12, pl. 1, figs. 10–17. 1897

Sporangium sessile, spherical, with one short papilla (occasionally two), of varying size, wall smooth, colorless; rhizoids very delicate, branched, arising from a short main axis; zoospores spherical, with a small centric globule and a long flagellum, escaping through pores formed upon the dissolution of the papillae; resting spore not observed.

Parasitic on the oöspores (and sporangia?) of *Pythium complens*, FRANCE.

Although the sporangia are said to be spherical the figures show wide variations from this shape, and it is difficult to decide just what form is to be considered typical. *Rhizophydiwm Pythii* was thought by de Wildeman to be perhaps only a form of *R. globosum*.

The fungus is said in the text of the original description to parasi-

tize the oöspores, whereas in the formal diagnosis it is said to be "sur les zoosporanges."

RHIZOPHYDIUM SPHAEROTHECA Zopf

Abhandl. Naturforsch. Gesell. Halle, 17:92, pl. 2, figs. 33-41. 1887

(Figure 11 D-E, p. 164)

Sporangia sessile, single or in groups, spherical or subspherical, with from two to five protruding papillae (one in smallest sporangia), small plants 4-5 μ in diameter, largest seldom exceeding 22 μ , wall smooth, colorless, distinctly double-contoured; rhizoidal system arising from a main axis, much branched; zoospores few in small sporangia, up to three hundred in large ones, spherical or ellipsoidal, 2.5-3 μ in diameter (see below), with a relatively large eccentric colorless globule 0.9-1.2 μ in diameter, a minute shining granule, and a delicate flagellum, emerging from the sporangia through comparatively large, circular, occasionally slightly protruding pores formed upon the deliquescence of the papillae, movement amoeboid as well as swimming; resting spore not observed.

On microspores of *Isoetes lacustris*, *I. echinospora*, causing fatty degeneration of the coarsely granular host protoplasm, pollen of *Pinus spp.* (*P. sylvestris*, etc.), Zopf (*op. cit.*, p. 82, pl. 1, figs. 1-6, 16 a-c), GERMANY; gymnospermous pollen, *Pseudotsuga mucronata* pollen, Graff (1928:161), pine pollen, Sparrow (1932b:275, fig. 2d), UNITED STATES; *Typha* pollen, Sparrow (1936a:441, pl. 17, fig. 16), ENGLAND.

The species differs from *Rhizophydiumpollinis-pini* primarily in the number and position of the pores, only a single terminal one being formed in *R. pollinis-pini*. As understood here, the species includes all "*Rhizophydiumpglobosum*" forms with multiporous, spherical, or subspherical sporangia and a branched rhizoidal system which inhabit the submerged microspores or microgametophytes of pteridophytes and spermatophytes. Certain of the plants considered *R. pollinis-pini* by Zopf (*loc. cit.*) and some later investigators fall within the limits of the species as here defined. The zoospores in the multiporous forms called *R. pollinis-pini* by Zopf varied from 4 μ to 6 μ in diameter, and the sporangia in some instances attained a diameter of 36 μ .

RHIZOPHYDIUM VAMPYRELLAE (Dang.) Minden

Kryptogamenfl. Mark Brandenburg, 5:320. 1911 (1915)

Chytridium Vampyrella Dangeard, Le Botaniste, 1:63, pl. 3, figs. 14-16.
1889.

Sporangium sessile, spherical, with a thickened smooth wall and several subapical discharge papillae; rhizoids branched, arising from a central somewhat thickened main axis; zoospores very narrowly ellipsoidal or ovoidal when escaping through the pores formed upon the deliquescence of the papillae, the conspicuous colorless globule anterior or basal, the flagellum of moderate length; resting spore (?) spherical, with a thick smooth wall and an apparently unbranched rhizoid, germination not observed.

On cysts of *Vampyrella* parasitizing colonies of *Gloeocystis vesiculosa*, FRANCE.

Considered doubtfully distinct from *Rhizophydiwm globosum* by Dangeard. The zoospores were observed to become very constricted and elongated when passing through the gelatinous layer of the colonies of *Gloeocystis*. Their shape during swimming evidently was not observed. In Dangeard's explanation of Plate 3 "Figure 16c" is referred to as a resting spore of the fungus. There is no such figure number, and it is assumed here that Dangeard meant Figure 16a.

The species is kept distinct for reasons mentioned in the discussion of *Rhizophydiwm globosum* (see p. 163).

RHIZOPHYDIUM CONSTANTINEANI Saccardo

Sylloge fungorum, 17:512. 1905

(Figure 11 F, p. 164)

Rhizophydiwm Vaucheriae Constantineanu, Revue Gén. Bot., 13:380, fig. 81. 1901. Non *Rhizophydiwm Vaucheriae* de Wildeman, Mém. Herb. Boissier, 1900 (15):6.

Sporangium sessile, spherical or subspherical, 6-8 μ in diameter, wall smooth, colorless; rhizoidal system very delicate, consisting of a few short branches which arise from a main axis; zoospores from four to six, spherical, 3.5 μ in diameter, with a colorless, eccentric globule,

escaping through a small apical pore and forming a temporary group attached to the pore by the tips of the flagella; resting spore not observed.

On filaments of *Vaucheria sp.*, RUMANIA.

The species has been discussed by Minden (1915:326) under *Rhizophyidium sphaerocarpum* (Zopf) Fischer. From the smaller size of its sporangia, however, and the branched nature of the rhizoids, it cannot without further study be referred to Zopf's fungus.

RHIZOPHYDIUM CYCLOTELLAE Zopf

Abhandl. Naturforsch. Gesell. Halle, 17:94, pl. 2, figs. 13-22a. 1887

(Figure 11 G, p. 164)

Sporangia sessile, single or in groups, subspherical or broadly obovate, up to 12μ in diameter, with a smooth delicate wall which collapses and disappears after spore discharge; rhizoidal system well developed, extremely delicate, with branches arising from a main axis; zoospores spherical, $1.8-2.5 \mu$ in diameter, with a relatively large eccentric colorless globule and a delicate flagellum, escaping through from one to three very small sessile pores, capable of amoeboid movement; resting spore not observed.

Parasitic on *Cyclotella sp.* in culture dishes; not capable of infecting *Melosira* or naviculoid or synedroid diatoms, pine pollen, or *Lycopodium* spores. Zopf (*loc. cit.*), in a *Stinkhaale* (= 'salt pool'?), GERMANY; *Cyclotella Chaetoceras*, Domján (1936:42, pl. 1, fig. 171), HUNGARY.

Infection always took place along the silica-free region between the girdle band and valve, obviating the necessity for penetration of the siliceous wall of the diatom. The contents of the latter, with the exception of the brown remains of the chloroplasts, were all consumed.

RHIZOPHYDIUM MACROSPORUM Karling

Bull. Torrey Bot. Club, 65:439, pl. 20, figs. 1-17. 1938

"Thalli eucarpic, numerous, gregarious. Zoosporangia hyaline, smooth, predominately spherical $22-110 \mu$, oval, broadly pyriform, and urceolate with 1 to 5, usually 2 or 3, low inconspicuous exit

papillae. Zoospores spherical 4.5–6 μ , hyaline, with an unusually large, 3–4 μ clear refractive globule and a 25–35 μ long cilium; occasionally becoming amoeboid; initial swarmspores emerging in a small globular mass surrounded by a hyaline matrix and lying quiescent for a few moments before separating; the remainder becoming active within the sporangium and emerging usually one by one. Rhizoidal system usually extensively developed, coarse, and branched, main axis occasionally 6 μ in diameter; delimited from the sporangia by a cross wall at maturity; arising from a single point or rarely from several places at the base of the sporangium. Resting spores hyaline, smooth, spherical, 15–30 μ , oval, 18 \times 20–33 \times 36 μ , or slightly irregular with a wall 1.5–2 μ thick, and one or more large refractive globules; germination unknown" (Karling, *loc. cit.*).

On cooked ground beef, dead cells of *Cladophora glomerata*, *Pithophora sp.*, *Nitella flexilis*, *Chara coronata*, root tips of *Allium cepa* and *Narcissus*, UNITED STATES.

RHIZOPHYDIUM ASYMMETRICUM (Dang.) Minden

Kryptogamenfl. Mark Brandenburg, 5:328. 1911 (1915)

(Figure 11 H, p. 164)

Chytridium asymmetricum Dangeard, Le Botaniste, 2:243, pl. 17, fig. 1. 1890–91.

Sporangium sessile, ovoid, 16 μ high by 10 μ in diameter, with a prominent slightly oblique apical papilla, wall stout, smooth, colorless; rhizoids delicate, branched, arising from a short slender main axis; zoospores very small, spherical, with an eccentric colorless globule and a fairly long flagellum, emerging through a pore formed upon the deliquescence of the papilla; resting spore not observed.

Parasitic on *Tribonema bombycinum* var. *minor*, FRANCE.

Considered by Fischer (1892:94) to be merely an irregular form of *Rhizophydiwm mammillatum* (Braun) Fischer. Minden (*loc. cit.*) though placing it in *Rhizophydiwm*, where, from its inoperculate type of discharge, it unquestionably belongs, briefly discusses it under *R. mammillatum*.

Because of the characteristically tilted papilla the species should be retained, at least for the present.

RHIZOPHYDIUM MAMMILLATUM (Braun) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):93. 1892 (sensu Dangeard, Le Botaniste, 2:242, pl. 16, fig. 32. 1890-91)

Chytridium mammillatum Braun, Monatsber. Berlin Akad., 1855:381; Abhandl. Berlin Akad., 1855:32, pl. 2, figs. 9-12. 1856.

Sporangium sessile, long-ovoid or narrowly to somewhat broadly citriform, with a more or less prominent apical papilla, 10-33 μ high by 10-22 μ in diameter, wall smooth, colorless, slightly thickened; rhizoids delicate, branched, short, arising from a slender main axis; zoospores spherical or somewhat ovoid, 2-4 μ in diameter, with a minute eccentric globule and a long flagellum, emerging through a small apical pore; resting spore not observed.

On *Coleochaete pulvinata*, Braun (*loc. cit.*), Schroeter (1885:190), swarm spores of *Stigeoclonium sp.*, Pringsheim (in Braun, 1856a), *Draparnaldia nudiuscula*, Rabenhorst (1868:280), GERMANY; *Draparnaldia sp.*, Dangeard (1890-91c:242, pl. 16, fig. 32), FRANCE; *Tribonema bombycinum*, de Wildeman (1890:18), BELGIUM; *Draparnaldia glomerata*, Serbinow (1907:158, pl. 4, figs. 29-34), RUSSIA; "Conferva," Valkanov (1931a:362), BULGARIA; oögonia of *Oedogonium sp.*, vegetative cells of *Draparnaldia sp.*, Couch (1932:251, pl. 15, figs. 36-39), UNITED STATES.

Neither Braun nor Pringsheim observed the endobiotic system or the zoospores of this species. Braun does state definitely, however, that the sporangium is inoperculate. Since these essential features are lacking in the original description the fungus described by Dangeard (*loc. cit.*) (and later by Serbinow) is taken as typifying the species. Schenk's fungus (1858a:236, pl. 5, figs. 1-5), termed *Chytridium mammillatum*, though like Braun's in the shape of its sporangium, possesses a peglike unbranched endobiotic part such as characterizes species of *Phlyctidium*. Actual discharge of the sporangium was not observed, and Schenk's fungus might well have been a *Chytridium*. Schenk remarks, however, that no opercula were found on the discharged sporangia, which, incidentally, were only one half the size of those described by Braun.

The specimen figured by de Wildeman (1891:170, fig. 1) and tentatively assigned to this species differs from it in having pyriform

sporangia and a small knoblike endobiotic part (see *Chytridium pedicellatum*, p. 357).

The fungus of Constantineanu (1901:379, fig. 80), found on *Spirogyra* in Rumania and called *Chytridium mammillatum*, possesses broadly ovoid, subspherical, or somewhat irregular bicornate sporangia and cannot be included in the present species. Further investigations may show it to be new.

Couch's fungus differs from Braun's and Dangeard's in having a broader, more prominent papilla or beak, and in the rhizoidal system, which arises from a short peglike axis rather than from a more elongate slender thread.

RHIZOPHYDIUM AMPULLACEUM (Braun) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):101. 1892

Chytridium ampullaceum Braun, Monatsber. Berlin Akad., 1855:384; Abhandl. Berlin Akad., 1855:66, pl. 5, figs. 24-27. 1856.

Olpodium ampullaceum (Braun) Rabenhorst, Flora Europaea algarum, 3:282. 1868.

Sphaerostylidium ampullaceum (Braun) Sorokin, Arch. Bot. Nord France, 2:20, fig. 17. 1883 (separate).

Sporangium sessile or, rarely, on a short stalk, spherical, 6-8 μ in diameter, with an apical discharge tube 4-5 μ long by 2 μ in diameter, wall thin, smooth, colorless; rhizoids feebly developed, branched; zoospores with a single globule and a posterior flagellum, discharged through the somewhat flaring funnel-like apex of the opened discharge tube; resting spore not observed.

Clustered on filaments of *Mougeotia* sp., *Oedogonium vesicatum*, *O. undulatum*, Braun (*loc. cit.*), GERMANY; on various algae, *Spirogyra*, *Cladophora*, Sorokin (1874b:6, pl. 1, figs. 6-11, and *loc. cit.*), EUROPEAN RUSSIA; *Oedogonium crassusculum* var. *idiosporum*, W. R. I. Cook (1932a:135, figs. 7-12), ENGLAND; *Oedogonium* sp., Atkinson (1909a: 338), *O. crenulato-costatum*, *O. plagiostomum*, *Mougeotia* sp., Graff (1928:159), UNITED STATES.

Braun considered the species a very doubtful member of the chytrids. This view has been shared by Petersen (1910:551, footnote), who believes the form should be entirely excluded from the chytrids and placed in the Infusoria. As has been pointed out by Graff

(*loc. cit.*), Petersen gives no reasons for this change. It is possible that Petersen is correct insofar as the form observed by Braun himself is concerned. The curious production of a delicate, scarcely visible, tilted conical prolongation of the discharge tube is not found on any other chytrid, and the general resemblance of Braun's figures to the immature stages of certain sessile choanoflagellates is very marked. Since the name has been applied by later investigators to what is unquestionably a chytrid, however, and since figures of spore discharge have been shown (see especially Sorokin, 1874b), it is probably best to retain Braun's species name.

RHIZOPHYDIUM ROSTELLATUM (de Wild.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):105. 1892

Chytridium rostellatum de Wildeman, Ann. Soc. Belge Micro. (Mém.), 14:19, fig. 6, 1890.

Sporangium sessile, ovoid, with a single subapical beaklike prolongation or, more often, with two opposite diverging ones, wall thin, smooth, colorless; rhizoidal system delicate, branched, arising from a short thin main axis; zoospores spherical, with a large globule, escaping through a pore formed at the tip of each beak of the sporangium; resting spore not observed.

On *Spirogyra crassa*, BELGIUM.

Resembling somewhat *Phlyctochytrium biporosum* Couch, but differing in the more pronounced beaks and in the nature of the rhizoidal system.

RHIZOPHYDIUM HAYNALDII (Schaarschmidt) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):92. 1892

Phlyctidium Haynaldii Schaarschmidt, Magyar Növénytani Lapok. Kolozsvár, 1883 (7):58, pl. 2; Hedwigia, 22:125. 1883.

Sporangium sessile, oblong-ovoid or pyriform, with rounded base, the apex bearing two broad diverging opposite tubular processes, generally of equal magnitude, which when strongly opposed give a triangular aspect to the sporangium; rhizoid delicate, unbranched; zoospores from eight to ten, ellipsoidal, 2μ long, with a long flagellum and a colorless eccentric oil droplet, escaping individually through

pores formed at the tips of the two apical processes, movement hopping; resting spore not observed.

On *Ulothrix zonata*, Schaarschmidt (*loc. cit.*), Scherffel (in Moesz, 1938:72), HUNGARY; (?) *Hormiscia uniflexa* (coll. Andrée), Lagerheim (1899:436), KING CHARLES LAND, ARCTIC REGION.

In the shape of its sporangium and the possession of two apical discharge pores the species resembles *Rhizophyllum rostellatum*, *Phlyctochytrium biporosum*, and *Rhizophyllum irregulare* (de Wild.) Fischer. Certain British specimens doubtfully placed in *Phlyctochytrium biporosum* by Sparrow (1936a:443, fig. 3 m-n, p) may belong here. Serbinow (1907:157) considers the species synonymous with *Rhizophyllum laterale*, but the configurations of the sporangia of the two species are totally unlike.

The record of Lagerheim (*loc. cit.*) is of doubtful validity. It is based on preserved material and is unsupported by figures or by an adequate description.

RHIZOPHYDIUM CHAETIFERUM Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:295. 1937; Papers Mich. Acad. Sci., Arts, Letters, 24, Pt. I:122, pl. 2, figs. 1-13. 1939

Sporangium spherical, rarely subspherical, colorless, predominantly 12 μ in diameter, the upper two thirds of the wall covered with long slender branched or unbranched hairs up to 30-50 μ in length; rhizoidal system delicate, profusely branched, arising from the tip of the slender penetration tube; zoospores spherical, 3 μ in diameter, with a single globule and a single posterior flagellum, discharged upon the deliquescence of an apical or subapical papilla, the aperture thus formed widening considerably after emergence of the spores; resting spore epibiotic, spherical or slightly subspherical, 12 μ in diameter, with a thickened wall covered by short processes, long hairs, or both, contents with a single large oil globule, rhizoidal system branched, germination not observed.

Saprophytic on *Cladophora*, *Oedogonium sp.*, UNITED STATES.

In the ornamentation of its sporangium the species resembles *Chytridium chaetophilum* Scherffel and *Phlyctochytrium chaetiferum* Karling. The resting spores resemble those of an imperfectly known species, *Rhizophyllum* (?) *setigerum* Scherffel (1925b:48, pl. 2, fig. 95).

RHIZOPHYDIUM CODICOLA Zeller

Publ. Puget Sound Biol. Station, 2:122, pl. 20, figs. 1-4. 1918

Sporangium sessile, spherical to almost obpyriform, 16-24 μ in diameter, with a smooth colorless relatively thick wall; rhizoidal system extensive, coarse, much branched, the ultimate branches delicate, arising from a stout irregularly expanded somewhat lobed main axis; zoospores spherical, 2.5-3 μ in diameter, with a colorless basal globule and a long flagellum, emerging through a large lateral irregular aperture in the sporangium wall; resting spore not observed. (Modified from Zeller.)

On *Codium mucronatum*, UNITED STATES (marine).

SECTION II¹

RHIZOPHYDIUM POLLINIS-PINI (Braun) Zopf, pro parte

Abhandl. Naturforsch. Gesell. Halle, 17:82, pl. 1, figs. 16-20. 1887
(Figure 11 J, p. 164)

Chytridium pollinis-pini Braun, Monatsber. Berlin Akad., 1855:381;
Abhandl. Berlin Akad., 1855:40, pl. 3, figs. 1-15. 1856.

Chytridium vagans Braun, Monatsber. Berlin Akad., 1856:588.

Phlyctidium vagans (Braun) Rabenhorst, Flora Europaea algarum, 3:278.
1868.

Phlyctidium pollinis (Braun) Sorokin, Arch. Bot. Nord France, 2:19,
fig. 13. 1883 (separate).

Phlyctidium pollinis-pini (Braun) Schroeter, Kryptogamenfl. Schlesien
3(1):190. 1885. (See p. 183.)

Sporangium sessile, spherical or nearly so, somewhat urceolate after discharge, with a more or less prominent fairly broad apical papilla, 10-25 μ in diameter, wall smooth, colorless, of variable thickness up to 1.4 μ ; rhizoids branched, arising from a more or less prolonged axis; zoospores spherical or ellipsoidal, 2-4 μ in diameter, with a colorless eccentric globule and a long flagellum, emerging singly and slowly through a broad apical pore formed upon the deliquescence of the papilla, movement hopping; resting spore sessile, spherical, 10-15 μ in diameter, with a smooth thick wall and a large globule; rhizoidal system branched, germination not observed.

¹ See also the following imperfectly known species of *Rhizophydiuum*:

R. Leptophrydis, p. 214

R. pyriformis, p. 212

R. persimilis, p. 212

Rhizophydiuum spp., pp. 212-214

Parasitic or saprophytic on floating pollen of *Pinus sylvestris*, Braun (*loc. cit.*), *Pinus spp.*, pollen of various angiosperms used as "bait" in water cultures (*Phlox*, *Tropaeolum*, *Helianthus*, *Populus*, etc.), Zopf (*loc. cit.*), pine pollen, Schroeter (1885:190), Sydow (Exsiccati: Sydow, Phyco. et Prot. 47; Mycoth. March. 4714), GERMANY; pollen of fir, Sorokin (1883:19, fig. 13), SOUTH RUSSIA; Maurizio (1895:14), SWITZERLAND; pollen of *Pinus sylvestris*, Valkanov (1931a:362), BULGARIA; pine pollen, Couch (1932:250, pl. 15, figs. 20-25), UNITED STATES.

The species with multiporous sporangia described by Zopf and widely reproduced as illustrative of *Rhizophyidium pollinis-pini* (see Fischer, 1892: fig. 16b; Migula, 1903: pl. 2 K, fig. 5; Fitzpatrick, 1930: fig. 20a) is here considered to be *R. sphaerotheca* (see p. 173). Since no description or figures were published of the form on *Tribonema bombycinum* collected by Itzigsohn (see Braun, 1856b:588) it cannot be compared with the present species. Presumably, there was a close resemblance, for Braun considered his fungus on pine pollen to be identical with it and thought, hence, that the species might more suitably be called *Chytridium vagans* than *C. pollinis-pini*. The fungus on pine pollen in France which Cornu (1872a:121) referred to *R. pollinis-pini* had endobiotic resting spores. These have been thought by Fischer (1892:89) to belong to one of several endobiotic Phycomycetes which also inhabit pollen grains. The fungus of Schenk (1858b:8) on *Chlamydomonas sp.* which was referred to this species is probably *R. globosum*. The chytrid briefly described by Serbinow (1907:156) as a facultative parasite of coniferous pollen grains was shown, when the rhizoids were stained, to be a species of *Phlyctidium* rather than of *Rhizophyidium*. See, however, the observations of Couch (*loc. cit.*) on the rhizoids, and see *Phlyctidium pollinis-pini*, on page 183.

Species of *Rhizophyidium* which attack the germinating oöspores of various members of the Peronosporaceae have been referred to *R. pollinis-pini* by Schroeter (1879:84) and by Melhus (1914:55, pl. 4). De Bary (1863:21) has also mentioned a "*Chytridium*" as parasitic on germinating oöspores of *Albugo*. It is evident from the description and figures of the fungus studied by Melhus that his material is not *R. pollinis-pini*. If the flagellation of the zoospores has been correctly observed it may be a species of *Rhizidiomyces*. Whether the other forms inhabiting peronosporaceous oöspores are

identical with Melhus' fungus cannot be ascertained. The latter may be described as follows:

Sporangium obpyriform or ovoid, up to 40μ in diameter, often narrowing at the base to form a short stalk, wall fairly thick, colorless, with a single apical or lateral papilla (occasionally two) $3-5 \mu$ in diameter; rhizoids fairly coarse, branched, arising from a central axis which is cylindrical or, sometimes, irregularly inflated; zoospores spherical or pyriform, 3μ in diameter, with a slightly eccentric colorless globule and an anterior flagellum 12μ in length, escaping individually and fully formed through an apical or lateral pore (occasionally two); resting spore (?) with a thick smooth yellow-brown wall, formed "inside the old sporangium," germination not observed.

? *Phlyctidium pollinis-pini* (Braun) Schroeter

Kryptogamenfl. Schlesien, 3 (1):190. 1885. Non Sorokin, Arch. Bot. Nord France, 2:19. 1883

Sporangium sessile, spherical, $20-25 \mu$ in diameter, with a slightly protruding apical papilla, wall fairly thick, with a faint reddish shimmer, contents colorless, with from one to two globules; zoospores about 2.5μ in diameter, with a colorless oil droplet, discharged through an apical pore.

On pine pollen, Schroeter (?), GERMANY.

Serbinow (1907:156) has asserted that a facultative parasite of pollen observed by him in Russia has sporangia which agree with Zopf's *Rhizophyidium pollinis-pini*, but which, in contrast to it, have an unbranched rhizoid. Since Zopf had both true *R. pollinis-pini* and what is called here *R. sphaerotheca* and since Serbinow did not further describe the sporangia of his organism, it is impossible to say what the latter observer had. It is evident, however, from Serbinow's emphatic statement, that a *Phlyctidium* species occurs on pollen. Schroeter's specific description is included here since it appears to be based, for the most part, on Braun's *Rhizophyidium pollinis-pini*. Because of Sorokin's previous application of *Phlyctidium* to Braun's fungus, Schroeter's combination cannot be used. A new name will be needed if Serbinow's observations are confirmed.

RHIZOPHYDIUM SCIADII (Zopf) Fischer

Rabenhorst. Kryptogamenfl., 1(4):94. 1892

(Figure 11 K, p. 164)

Rhizophyton Sciadii Zopf, Abhandl. Naturforsch. Gesell. Halle, 17:91,
pl. 2, figs. 23-32. 1887.

Sporangium sessile, at first spherical or somewhat flattened at the base, at maturity pyriform, with a broad blunt apex (the papilla), up to 20μ high by 17μ in diameter, walls smooth, colorless, slightly thickened; rhizoidal system extensive, arising from one or two main axes, richly branched; zoospores as many as eighty to one hundred in the larger sporangia, spherical or ellipsoidal, $2.3-4 \mu$ in greatest diameter, with a relatively large ($1-1.3 \mu$ in diameter) refractive slightly eccentric colorless globule and a very delicate flagellum, emerging upon the deliquescence of the thin-walled blunt apex of the sporangium; resting spore not observed.

Parasitic on *Ophiocytium (Sciadium) arbusculum* in fresh and salt water (in culture dishes), GERMANY.

In attacked plants the plasma, nucleus, and chromatophore were destroyed, the residue of the latter forming yellow-brown or dirty red-brown clumps or granules in the cell. Staining was necessary to demonstrate the full extent of the rhizoidal system.

RHIZOPHYDIUM SCHROETERI de Wildeman

Mém. Herb. Boissier, 1900 (15):5, fig. 3; Bull. Acad. Roy. Belg. (Sci.), V, 17:289, fig. 3. 1931

Sporangium sessile, spherical, ellipsoidal, or ovoid, up to 7μ in diameter, with a prominent apical or subapical papilla, wall smooth, colorless; endobiotic system very delicate, consisting of an unbranched or once-branched rhizoid; zoospores rarely more than twelve, spherical, about 1μ in diameter, with an eccentric globule, escaping upon the dissolution of the papilla, the wall of the empty urceolate sporangium disintegrating after discharge; resting spore not observed.

On *Asterionella gracillima*, coll. Schroeter, SWITZERLAND.

Considered by Minden (1915:326) to be probably a small form of *Rhizophydiump sphaerocarpum*, which it resembles in its general aspect.

One of the sporangia shown by de Wildeman (1931: fig. 3) is borne on a short needle-like stalk.

RHIZOPHYDIUM SPAEROCARPUM (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):95. 1892

(Figure 11 L-M, p. 164)

Rhizidium sphaerocarpum Zopf, Nova Acta Acad. Leop.-Carol., 47:202, pl. 19, figs. 16-27. 1884.

Sporangium sessile, subspherical, ovoid, or urceolate, with a broad (4-7 μ in diameter) protruding apical papilla, 6-18 μ in diameter and up to 20 μ high, wall colorless, smooth, of two layers, the outer thicker than the inner; endobiotic part consisting of a slender, generally unbranched rhizoid; zoospores spherical or ovoid, 1.5-2 μ in diameter, from a few to forty in a sporangium, with a colorless centric or slightly eccentric globule and a long flagellum, emerging in an evanescent vesicle, movement amoeboid or hopping; resting spore sessile, spherical, about 11-18 μ in diameter, with a thick smooth colorless wall, contents with a large eccentric globule, rhizoid like that of the sporangium, germination not observed.

On *Spirogyra*, *Mougeotia*, *Oedogonium*, and other algae, Zopf (*loc. cit.*), GERMANY; *Mougeotia genuflexa* (coll. Marchal), de Wildeman (1890:13, fig. 3), BELGIUM; *Mougeotia parvula*, Atkinson (1909a: 326, fig. 3 a-g), *M. sphaerocarpa*, *Mougeotia* sp., Graff (1928:161), UNITED STATES; *Oedogonium* sp., Skvortzow (1925:430), MANCHURIA; *Spirogyra* sp., *Gonatонema* sp., Tokunaga (1934b:390, pl. 11, figs. 6, 8-9), JAPAN.

This species, like *Rhizophydiumplobosum*, has become a collective one, and a number of fungi with ovoid, spherical, or urceolate sporangia which possess a broad discharge papilla have been referred to it. The above diagnosis does not include types with a well-developed much-branched rhizoidal system or those growing on organisms other than algae. These limitations may subsequently be shown to be too restrictive and the extent of rhizoidal development a poor specific character (see, for example, *Chytridium Lagenaria*, p. 348).

The following have been excluded:

1. De Wildeman (1893b:61, pl. 6, figs. 13-16, pl. 7, fig. 18), on *Mougeotia* and *Spirogyra*, BELGIUM. The sporangia resemble those

of the present species, but no rhizoidal system was observed. De Wildeman noted that on *Mougeotia* the fungus caused marked bending of the host cells.

2. Raitschenko (1902:124, figs. 1-8), on the heterocysts of *Anabaena Flos-aquae*, RUSSIA. The endobiotic part is a stout unbranched peg (see *Phlyctidium megastomum*, sp. nov., p. 148).

Valkanov (1931a:362, fig. 1), on *Mougeotia* sp., BULGARIA. From the figures, the sporangia are nearly or completely spherical and the rhizoids much branched. No discharge of the zoospores was observed. The fungus stimulated the host to form a protective plug of wall material.

4. Skvortzow (1927:206), on *Spirogyra*, MANCHURIA. No mention is made of the character of the rhizoids.

5. Sparrow (1933c:519, pl. 49, fig. 1; 1936a:442, pl. 19, figs. 15-18), on nematodes, UNITED STATES, ENGLAND. Though resembling *Rhizophydium sphaerocarpum* in the shape of its sporangium, in its rhizoid, and in the method of spore discharge, Sparrow's fungus differs in several particulars. The zoospores in both the American and the British collections were about 4-5 μ in diameter and formed in a thin-walled sporangium, whereas, to judge from Zopf's figures, the sporangium is thick-walled and the zoospores are estimated to be about 2.5 μ in diameter. Another difference is the type of substratum. How far we are justified in supposing that a single species of chytrid is capable of penetrating all types of walls—cellulose, chitinous, or siliceous—cannot at present be said with certainty. *R. gibbosum*, the peculiar sporangia of which cannot be confused with those of any other species, was observed by Zopf on both diatoms and rotifer eggs, and *Catenaria*, another chytrid, has been grown on both plant and animal substrata (Karling, 1934a). Arbitrarily, however, and with some justification on morphological and physiological grounds, the inhabitant of nematodes is segregated for the present from *R. sphaerocarpum* (see *R. vermicola*, sp. nov., p. 188).

6. Domján (1936:42, pl. 1, figs. 3-4, 13, 26), on *Spirogyra*, *Zygnuma*, and *Closterium*, HUNGARY. The sporangia and resting spores resemble somewhat those of *Rhizophydium sphaerocarpum*, but the rhizoidal system is richly branched and extensive.

7. Tokunaga (*loc. cit.*, pl. 11, fig. 7), on *Cladophora* sp., JAPAN. The rhizoids are too richly branched for this species. The fungus resembles closely Miss Domján's organism.

The chytrid supposed by Dangeard (1890-91c:244, pl. 16, fig. 9)

to be Zopf's species and called *Chytridium sphaerocarpum* by Dangeard is operculate and has been retained in *Chytridium*.

RHIZOPHYDIUM VAUCHERIAE de Wildeman

Mém. Herb. Boissier, 1900 (15):6; Bull. Acad. Roy. Belg. (Sci), V, 17:285,
fig. 1, 1-10. 1931

Sporangium sessile, spherical, 26-50 μ in diameter, with a broad prominent apical papilla, wall somewhat thickened, colorless, smooth; endobiotic part consisting of an unbranched rhizoid; zoospores spherical, 1.5 μ in diameter, with a conspicuous colorless globule, escaping successively through a large apical pore formed upon the dissolution of, or rarely the dehiscence of, the apical papilla, the empty sporangium strongly urceolate, the irregular discharge pore with a slightly recurved margin; resting spore not observed.

Parasitic, often in large numbers, on the oögonia of *Vaucheria sessilis*, coll. Massart, BELGIUM.

Further observations on the process of zoospore discharge are necessary. Typically, the conspicuous papilla is dissolved, but on rare occasions it is said to persist and to be thrown back as a sort of operculum. De Wildeman believes dissolution of this cap occurs at a varying rate, depending upon conditions in the medium. The fungus is of interest because of the significance of the type of sporangial discharge in relation to our present concept of genera. The situation is evidently similar to that found in *Blastocladia Pringsheimii* (Sparrow, 1932b:291), where a cap is often observed for a short time at the apex of the mass of emerging zoospores but more often dissolves completely before the swarmers are discharged.

De Wildeman believes the species to be near *Rhizophydiump sphaerocarpum*.

The wall of the egg was often stimulated to thicken around the rhizoid of the parasite. The vegetative cells were not attacked, nor was pollen of *Alnus* and *Salix* occurring in the water with the alga.

RHIZOPHYDIUM CARPOPHILUM (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):95. 1892

Rhizidium carpophilum Zopf, Nova Acta Acad. Leop.-Carol., 47:200,
pl. 20, figs. 8-16. 1884.

Sporangia sessile, often clustered, at first spherical or ovoid, becoming somewhat pyriform after discharge, 9.6-25.2 μ in diameter,

wall thin, smooth, colorless; endobiotic part consisting of a tenuous unbranched or sparingly branched rhizoid; zoospores two to forty or more, spherical or slightly ellipsoidal, 3-6 μ in diameter, with a colorless eccentric globule and a very long flagellum, emerging through an apical fairly broad slightly elevated pore, movement swimming or amoeboid; resting spore sessile, spherical, 5-9 μ in diameter, with a slightly thickened smooth wall and a large colorless oil globule, germination not observed.

On oögonia and oöspores of *Saprolegnia* sp., *Achlya* sp., etc. Occurring in clusters of one hundred or more on a single oögonium, Zopf (*loc. cit.*), GERMANY; (?) on sporangium of *Olpidiopsis Saprolegniae*, Sparrow (1932b:276, text fig. 1b), oögonia and oöspores of *Saprolegnia* sp., *Achlya* sp., oöspores of *Monoblepharis macrandra*, Sparrow (1933c:519), UNITED STATES; oögonia of *Achlya racemosa*, Tokunaga (1934b:389, pl. 11, fig. 3), JAPAN; eggs of *Achlya* sp., *Dictyuchus monosporus*, oöspores of *Monoblepharis macrandra*, Sparrow (1936a:442, pl. 17, figs. 4-5), ENGLAND.

The fungus is a very virulent parasite and soon destroys the eggs of the host. Zopf noted that if oöspores were not already differentiated in the oögonia when the attack occurred, the contents of the infected oögonium contracted into a ball of fatty material.

The species, while common in gross water cultures of higher Phycomycetes, is for the most part found after vigorous growth of the host plant has ceased. It has been cultivated on agar, pollen grains, and boiled maize stems by Couch (1939a).

The organism termed *Rhizophydium carpophilum* by Coker (1923:186, pl. 62, figs. 11-13) differs in certain essential features, particularly in the possession of an inflated rhizoid. It may be a species of *Phlyctochytrium*. No zoospore discharge occurred in the form observed by Sparrow on *Olpidiopsis*, which was in turn parasitizing a species of *Achlya*, and hence its generic disposition is doubtful.

RHIZOPHYDIUM VERMICOLA, sp. nov.¹

(Figure 11 N, p. 164)

Sporangium sessile, spherical, urceolate after discharge, 15-20 μ in diameter, with a broad apical papilla, wall thin, smooth, colorless;

¹ *Rhizophydium vermicola*, sp. nov.—Sporangium sessile, sphaericum, post rupcionem urceolatum, 15-20 μ diam.; papilla lata, apicali; membrana tenui, levi, hyalina;

endobiotic part consisting of a slender unbranched rhizoid; zoospores spherical, about $4-5 \mu$ in diameter, with a colorless eccentric globule and a long flagellum, emerging apparently imbedded in a gelatinous matrix or surrounded by a vesicle through a wide apical pore formed upon the deliquescence of the papilla, soon assuming individual motility and swimming away; resting spore not observed.

On *Anguillula* infected by other fungi, Sparrow (1933c:519, pl. 49, fig. 1), UNITED STATES; Sparrow (1936a:442, pl. 19, figs. 16-18), ENGLAND.

In both cases the chytrid was found on worms harboring other fungi. In the American material it occurred with *Harposporium Anguillulae*, and in the British with undetermined species of *Lagenidium* and *Aphanomyces*.

The fungus has previously been discussed as *Rhizophydiump sphaerocarpum* (Zopf) Fischer, but differs from this species in certain minor features (see p. 186). Buckley and Clapham (1929:6, text figs. 19-21, pl. 1, figs. 1-3) have described as *R. carpophilum* a fungus on eggs of *Dibothriocephalus latus* (a helminth), in England, which may possibly be referable to the present species. The sporangia were larger (up to 35μ in diameter), and the main rhizoid formed delicate branches at its tip. The zoospores, however, were the same size ($4.5-5 \mu$) as those of *R. vermicola*.

RHIZOPHYDIUM MISCHOCOCCI Scherffel

Arch. Protistenk., 54:195, pl. 9, fig. 56. 1926

(Figure 11 R, p. 164)

Sporangium sessile, broadly pyriform, with a thin smooth colorless wall, 5μ high by 5μ in diameter (at the base); endobiotic system consisting of a long, fairly thick, unbranched rhizoid; zoospores four, each with a fairly large colorless globule, escaping through an apical pore, the wall of the sporangium collapsing after discharge, motile zoospores not seen; resting spore not observed.

On *Mischococcus confervicola*, HUNGARY.

parte endobiotica tenui, simplici, rhizoidea; zoosporis rotundis, ca. $4-5 \mu$ diam., globulo hyalino eccentrico et cilio longo praeditis, emergentibus ut videtur a matrice gelatinosa vel vesicula circumdati per porum papillae deliquescentia formatum, mox motabilibus natantibus; sporis resistantibus nondum visis.

In *Anguillulis* quae fungis variis infesta sunt, UNITED STATES, ENGLAND.

Scherffel asserted that if *Phlyctidium* is segregated from *Rhizophydium*—which he does not favor—his fungus more properly belongs in the former genus. It is retained here because its slender rhizoid is uninflated and not *haustorial*, as in typical *Phlyctidium*.

RHIZOPHYDIUM AGILE (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):96. 1892

Rhizophyton agile Zopf, Nova Acta Acad. Leop.-Carol., 52:343, pl. 20, figs. 1-7. 1888.

Sporangia occurring singly or in groups on the surface of the gelatinous sheath of the host, sessile, variable in shape, broadly pyriform, sometimes somewhat angular and blunt-cornered, usually not over 10-15 μ in diameter, often having a narrow conical base, with a small nearly sessile or slightly protruding apical papilla, wall colorless, smooth, delicate, collapsing and disintegrating after spore discharge; rhizoids richly branched, arising from the tip of a single stalk which passes through the gelatinous sheath of the host; zoospores not over fifty, spherical, with a single slightly eccentric colorless globule and occasionally from one to two smaller ones, flagellum delicate, movement quick, in zigzag lines, or amoeboid; resting spore not observed.

Parasitic on *Chroococcus turgidus*, causing an epidemic both in the field and in gross culture that destroys up to 75 per cent of the individuals, Zopf (*loc. cit.*), GERMANY; Serbinow (1907:159, pl. 4, figs. 35-36), RUSSIA.

The parasite caused a swelling of the gelatinous sheath and a quick discoloration of the cell contents. The latter became olive green, then dirty yellow brown.

Serbinow noted that the fungus was a facultative parasite or even a true saprophyte. The sporangia figured by him are more regularly pyriform than those in Zopf's organism, and the rhizoid is an apparently unbranched slender thread. In these characters it approaches *Rhizophydiun simplex* (Dang.) Fischer.

RHIZOPHYDIUM ACUFORME (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):93. 1892

Rhizidium acuforme Zopf, Nova Acta Acad. Leop.-Carol., 47:209, pl. 21, figs. 33-44. 1884.

Sporangium sessile, broadly pyriform, 6-16 μ in diameter, with a

single apical papilla, wall thin, smooth, colorless; rhizoids delicate, sparingly branched, arising from a main axis; zoospores about 2–2.5 μ in diameter, with a single colorless globule, escaping through an apical pore formed upon the deliquescence of the papilla; resting spore sessile, spherical, generally smaller than the sporangium, with a smooth thickened wall, the contents bearing a large globule, rhizoids delicate, sparingly branched, arising from a main axis, germination not observed.

Parasitic on moving cells of a *Chlamydomonas*-like alga, Fischer (*loc. cit.*), GERMANY; *Chlamydomonas* *sp.*, de Wildeman (1890:9), BELGIUM; (?) *Palmodictyon* *sp.*, Couch (1932:251, pl. 15, figs. 26–35; see below), UNITED STATES.

Zopf's material was found in March, while the ice was still on the pond and the temperature of the water was 11°–13° Réaumer. Up to ten chytrids were found on a single zoospore of the host. De Wildeman (*loc. cit.*) noted that the host cell continued to move even when infected by as many as six zoospores of the chytrid. In these instances, however, the sporangia of the parasite did not mature. In the early stages of development the fungus had no visible effect on the alga, but as the parasite matured the host lost its motility and finally succumbed to the invader.

The form described by Couch (*loc. cit.*) on *Palmodictyon* *sp.* differs in certain essential features from that of Zopf. Its sporangia are smaller (6.2–9 μ in diameter) and the discharge papilla, which may be subapical or even lateral, is much broader and longer (up to one half as long as the diameter of the sporangium). Furthermore, certain sporangia formed zoospores about one half the size of those formed by other sporangia. Couch (*loc. cit.*) considers the organism to be intermediate between *Rhizophydiuum acuiforme* and *R. minutum* Atkinson.

RHIZOPHYDIUM MINUTUM Atkinson

Bot. Gaz., 48:328, fig. 4. 1909

"Zoosporangia obpyriform or flask-shaped, broadly papillate, 5–6 μ in diameter, sessile with a few slender rhizoidal filaments at the base in the host cell. Apex opening by a single pore. Zoospores two to four in a zoosporangium, oval, uniciliate, with a single oil drop, 2.5 μ in diameter" (Atkinson, *loc. cit.*).

On *Spirogyra varians*, UNITED STATES.

RHIZOPHYDIUM EUDORINAE Hood

Proc. Birmingham Nat. Hist. and Phil. Soc., 12:45, figs. 1-5. 1910; Trans. Brit. Mycol. Soc., 5:236, figs. 1-4. 1916

Sporangium imbedded in the gelatinous sheath of the host colony, sessile on the cell, broadly pyriform with a prolonged neck, the broad apex extending slightly beyond the outer surface of the gelatinous sheath, 20-35 μ high by 10-17 μ in diameter, wall thin, smooth, colorless; rhizoid delicate and unbranched; zoospores numerous, ovoid, 2 μ in diameter, with a minute colorless eccentric globule and a single flagellum, emerging from the apex of the sporangium in a compact irregular mass imbedded in mucilaginous material from which, after a period of rest, they escape; resting spore within the gelatinous sheath, supported by a short stalk on the host cell, asexually formed, spherical, 10-16 μ in diameter, with a thick dark rough wall, germination not observed.

Parasitic on *Eudorina elegans*, ENGLAND.

The development of this species is similar to that of *Phlyctidium Eudorinæ*. The zoospore comes to rest on the surface of the gelatinous sheath of the host colony and produces a slender threadlike penetration tube which pierces the sheath and becomes attached to the nearest algal cell. Miss Hood states that branches of the thread may penetrate two adjacent cells and that two zoospores may have one thread in common. The latter statement seems very improbable. After attachment to the algal cell the body of the zoospore enlarges and is drawn gradually within the gelatinous sheath, so that often the mature sporangium is sessile on the host cell, with its apex slightly protruding from the sheath. The character of the rhizoid within the host cell is not mentioned. From the description and the figures given, presumably that part of the infection tube within the sheath expands and forms the lateral walls of the sporangium. A somewhat similar type of development is found in *Dangeardia*, which differs, however, from *Rhizophydiwm Eudorinæ* primarily in having resting spores formed within the contents of the algal cells.

RHIZOPHYDIUM BRAUNI (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):94. 1892

Chytridium Brauni Dangeard, Bull. Soc. Bot. France, 34:xxii. 1887;
Le Botaniste, 1:57, pl. 3, fig. 11. 1889.

Sporangium sessile on the gelatinous envelope of the algal colony, narrowly pyriform or ovoid, the attenuated apex often slightly curved, wall stout, smooth, colorless; rhizoid a long slender unbranched (?) filament which penetrates the algal cells; zoospores from fifteen to twenty-five, spherical, 2μ in diameter, with an eccentric colorless globule and a long flagellum, escaping through an apical pore formed upon the deliquescence of a papilla; resting spore not observed.

Parasitic on *Apiocystis Brauniana*, FRANCE.

If subsequent investigations show that the rhizoid is unbranched within the algal cells and does not taper, then the species might better be placed in *Phlyctidium*. The sporangia are described by Dangeard as ovoid, but from the figures they appear distinctly narrowly pyriform. *Rhizophydiump simplex* seems doubtfully distinct from this species.

RHIZOPHYDIUM SIMPLEX (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):101. 1892

(Figure 11 S, p. 164)

Chytridium simplex Dangeard, Le Botaniste, 1:60, pl. 3, figs. 18-20. 1889.

Sporangium resting directly on the host cell or on the surface of the gelatinous sheath, narrowly pyriform, $8-15 \mu$ long by $6-7 \mu$ in diameter, prolonged apically into a slightly bent tube, wall thickened a little, smooth, colorless; endobiotic part consisting of an unbranched rhizoid which penetrates the protoplasm of the host; zoospores few to from thirty to forty, ellipsoidal or spherical, $1.5-3 \mu$ in diameter, with a colorless basal globule and a long flagellum, emerging through a small pore formed at the tip of the sporangium; resting spore spherical, $6-7 \mu$ in diameter, with a thick smooth colorless wall, rhizoidal system like that of the sporangium; germination not observed.

Parasitic on cysts of *Cryptomonas* sp. in culture jar, Dangeard (*loc. cit.*), FRANCE; dead colonies of *Pandorina*, Sparrow (1933c:519), UNITED STATES; *Spirogyra*, *Chlorococcum* (?), Sparrow (1936a:439, fig. 3 h-k), ENGLAND.

Dangeard observed that changes in the host contents quickly occurred after infection by the fungus. The olive-colored plasma was

reduced to reddish granules and the cellulose wall lost its structure and expanded. The swarmers of the alga were not attacked.

The British material differed from Dangeard's species in having fewer and larger (3μ in diameter rather than 1.5μ) zoospores formed in the sporangium. Certain of the sporangia appeared to show internal proliferation, but owing to the small size of the structures involved this could not be determined with absolute certainty.

Perhaps only doubtfully distinct from *Rhizophydisum Brauni*.

RHIZOPHYDIUM PSEUDODISTOMUM Scherffel

Abstracts of Communications, V Inter. Bot. Congress, Cambridge, 1930:222;
Arch. Protistenk., 73:140, pl. 9, fig. 2 a-b. 1931

Sporangium sessile, distinctly pyriform, with a broad convex base and a prominent apiculus, $16-20 \mu$ high by $13-18 \mu$ in diameter, wall thin, smooth, colorless; rhizoids well developed, branched; zoospores not observed, apparently emerging through a discharge tube 2μ long by 5μ in diameter which forms subapically on the sporangium, the apiculus becoming slightly lateral as a consequence; resting spore not observed.

Parasitic on *Oocystis solitaria* var. *Wittrockiana*, HUNGARY.

The parasite soon destroyed the contents of the host cell and reduced them to a reddish-brown mass.

The unnamed fungus found on *Protoderma* from North Africa by Sparrow (1938a:147, fig. 2a) with a pyriform sporangium bearing two prominent apical papillae may possibly be referable to this species. The endobiotic system consisted, so far as could be observed, of a short peglike structure, but whether this gave rise distally to branches was not determined.

RHIZOPHYDIUM GRANULOSPORUM Scherffel

Arch. Protistenk., 53:44, pl. 2, figs. 81-86. 1925

(Figure 11 P-Q, p. 164)

Sporangium sessile, broadly pyriform, with a broad apex, $7-14 \mu$ high by $5-9 \mu$ in diameter, usually appearing tilted on the surface of the host, wall thin, smooth, colorless; rhizoids extremely delicate, feebly developed, arising from a short main axis; zoospores ovoid, 3μ long by 2μ in diameter, with a large colorless slightly eccentric globule and a long flagellum, escaping through a broad pore formed upon the dissolution of an apical, subapical, or occasionally lateral

papilla; resting spore spherical, 5–7 μ in diameter, wall thick, colorless, moderately covered with short rodlike protuberances, resting on the apex or side of the companion cell, germination not observed; companion cell single (rarely two), spherical or turbinate, smooth-walled, 2.5–3 μ in diameter, sessile or with a short extramatrical stalk, rhizoid unbranched.

Parasitic on *Tribonema bombycinum*, Scherffel (*loc. cit.*), HUNGARY; Sparrow (1939a:124, pl. 2, figs. 14–25), UNITED STATES.

In the American material both conjugating thalli appeared to develop on the host wall, although in two instances the receptive thallus seemed to make contact only with the "male" plant. Once the "female" alone was attached to the algal cell. It was observed that the characteristic spines appeared on the receptive thallus soon after fertilization and before thickening of the wall had been initiated.

RHIZOPHYDIUM VERRUCOSUM Cejp

Bull. Internat. Acad. Sci. Bohême, 42(3):4, pl. 1, figs. 9–10, pl. 2, fig. 2.
1933 (separate)

Sporangium sessile, narrowly pyriform or ovoid, almost citriform, 14–22 \times 32–41 μ (high?), wall stout, its outer surface densely covered by warts, with a prolonged slightly curved smooth apiculus (papilla?) 12 μ long by 7 μ in diameter; rhizoidal system delicate, composed of short branches; zoospores spherical, 2–3 μ in diameter, with a single globule, uniflagellate, undergoing a period of rest (outside?) before swarming; resting spore subspherical, rarely irregular, 25–30 μ in diameter, with a thick wall covered with coarse warts, contents with numerous oil globules, rhizoids not observed, germination not observed.

On *Closterium sp.*, GERMANY.

RHIZOPHYDIUM ZOOPHTHORUM (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):94. 1892

(Figure 11 O, p. 164)

Chytridium zoophthorum Dangeard, Bull. Soc. Bot. France, 34:xxii. 1887;
Le Botaniste, 1:58, pl. 3, figs. 10, 21. 1889.

Sporangia sessile, often in clusters, ovoid or somewhat pyriform, with a prominent apiculus, 20–25 μ long by 15–17 μ in diameter, wall thin, smooth, colorless; rhizoids extensive, richly branched, arising as secondary branches from a main axis; zoospores ovoid, 3 μ (long?),

with dense granular plasma, a slightly refractive colorless basal globule, and a flagellum 30μ in length, escaping through a narrow pore formed at the tip of the apiculus; resting spore not observed.

Parasitic on adults and eggs of rotifers, Dangeard (*loc. cit.*), FRANCE; liver-fluke eggs (coll. J. Bayley Butler), Sparrow, IRELAND.

The habitat, ovoid sporangium with prominent apiculus, and richly branched rhizoidal system are distinctive features of this species. The living material from Ireland, on liver-fluke eggs, was kindly sent for examination by Professor Bayley Butler, of University College, Dublin, in 1933. Other eggs were infected by *Catenaria* and a fungus similar to *Rhizophydiwm globosum*. The thalli of the present species frequently formed dense clusters at the operculate apex of the fluke eggs. A similar gregarious habit was noted by Dangeard on rotifer eggs.

SECTION III¹

RHIZOPHYDIUM CLINOPUS Scherffel

Abstracts of Communications, V Inter. Bot. Congress, Cambridge, 1930:222;
Arch. Protistenk., 73:141, pl. 9, fig. 3 a-g. 1931

(Figure 11 T, p. 164)

Sporangium sessile on the raphe of the host, obovoid or obpyriform, with a broad more or less sharply defined stalklike basal part which is inclined somewhat to the long axis of the main body of the sporangium, with which it is continuous, wall smooth, delicate, $11-24 \mu$ in diameter by $6-17 \mu$ high, usually $16-18 \mu$ in diameter by $8-10 \mu$ high; rhizoid unbranched, 1μ in diameter; zoospores formed in large numbers, spherical, 3μ in diameter, with a colorless globule 1μ in diameter and a long flagellum, released upon the deliquescence of the entire upper half of the sporangium wall, movement hopping or amoeboid; resting spore (?) sessile, subspherical, with a flattened base, 8μ in diameter, wall thick, smooth, colorless, contents with a colorless refractive oil globule, 5μ in diameter, endobiotic part enclosed in a plug of host wall material, germination not observed.

On moribund diatoms, *Cymatopleura elliptica*, *C. solea*, *Nitzschia sigmoidea*, *Cymbella*, *Navicula* sp., HUNGARY.

¹ See also the imperfectly known species *Rhizophydiwm septocarpoides*, p. 214, and *R. Lecythii* Ingold (*Trans. Brit. Mycol. Soc.*, 25:45, 1941).

The resting spores, found only on *Nitzschia sigmaoidea*, have not been connected with certainty to the sporangial stage.

The species resembles *Rhizidiopsis* in the possession of a poorly defined fertile basal region on the sporangium, and may ultimately be referred to this genus. It differs from *Rhizidiopsis emmanuelensis* in its method of spore discharge, that is, discharge by the deliquescence of the upper part of the sporangium, and in having a smooth-walled resting spore.

RHIZOPHYDIUM ECHINATUM (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4): 96. 1892

Chytridium echinatum Dangeard, Journ. de Botanique, 2:143, pl. 5, figs. 11-15. 1888.

Sporangium sessile, very broadly obovate with a strongly obtuse somewhat lobed apex, urceolate at maturity, 13.5μ high by 10.8μ in diameter (at apex?), wall thin, smooth, colorless; rhizoidal system consisting of an unbranched short tapering stalk; zoospores spherical, 2.5μ in diameter, with a basal colorless globule and a long flagellum, emerging through a very broad apical opening with a reflexed rim and forming a compact temporary mass surrounded by mucous; resting spore sessile, spherical or subspherical, 10μ in diameter, with a thick wall covered with somewhat long colorless stout spines, contents coarsely granular, yellowish, with a large oil globule, germination not observed.

Parasitic on *Glenodinium cinctum*, FRANCE.

There is some question as to the method of zoospore discharge in this species. Fischer and Minden have considered it to occur inoperculately and have placed the organism in *Rhizophydiuum*. Dangeard says of the discharge that the "... partie terminale du sporange s'enlevant en forme de calotte pour la sortie des zoospores." Though the word "opercule" is not used here, he clearly states that the top of the sporangium is lifted up by the emerging spores, and the sharply defined reflexed rim of the open sporangium gives additional evidence that such has been the case. In contrast to those of most species of *Chytridium*, however, the resting spores—if indeed they belong to the fungus—are epibiotic, as in *Zygorhizidium*, but, unlike those of *Zygorhizidium*, they are apparently asexually formed.

Possibly belonging in *Phlyctidium*.

RHIZOPHYDIUM OVATUM Couch

Mycologia, 27:168, figs. 28-55. 1935

(Figure 2 B-F, p. 46)

Sporangium sessile, obpyriform or obovoid, broadest in the distal half, with a broad apical papilla, $8.4-16.8 \times 16-30 \mu$ (mostly $13 \times 20-25 \mu$), wall fairly thin, smooth, colorless; rhizoid (possibly two) very short and delicate, arising from a minute bulbous main axis; zoospores (gametes?) somewhat ovoid, $3 \times 4 \mu$, with a large colorless eccentric oil globule and a long flagellum, emerging with great rapidity through an apical pore formed upon the deliquescence of the papilla and swimming away; resting spore spherical, $5.4-9.6 \mu$ (mostly 8.4μ) in diameter, with a slightly thickened smooth colorless wall and a large slightly eccentric colorless globule, sexually formed, the motile female gamete coming to rest and encysting on the upper surface of an undeveloped spherical ($3.6-5 \mu$ in diameter), subspherical, or ovoid ($5.4-9.6 \mu$ in diameter) male thallus, which is provided endobiotically with a small bulbous swelling and a short rhizoid, both then increasing somewhat in size, especially the more distal female structure, which eventually receives the contents of the male, expands, and becomes transformed into the resting spore, the latter germinating after a short resting period (from two to three days) to form zoospores. (Modified from Couch.)

On *Stigeoclonium* sp., UNITED STATES.

Couch was unable to determine whether the gametes were borne in sporangia with the zoospores or formed in separate gametangia (see under "Sexual Reproduction," p. 48). The species is a very interesting one, and further investigations on the nature and fate of the motile bodies produced by the germinating resting spore and on the cytological details of germination would be of greatest value.

SECTION IV¹

RHIZOPHYDIUM TRANSVERSUM (Braun) Rabenhorst

Flora Europaea algarum, 3:281. 1868

Chytridium transversum Braun, Monatsber. Berlin Akad., 1855:382;
Abhandl. Berlin Akad., 1855:44, pl. 4, figs. 1-6. 1856.

¹ See also the following imperfectly known species of *Rhizophydiuum*: *R. astero-sporum*, p. 215; *R. Barkerianum*, p. 215; *R. Spirotaeniae*, p. 216.

Sporangium sessile, at first spherical, becoming broadly ellipsoidal or fusiform, the apices strongly papillate, slightly curved at maturity, up to 16.6μ in diameter, with its long axis perpendicular to its point of insertion on the algal cell; endobiotic part so far as observed consisting of a slender unbranched rhizoid; zoospores ellipsoidal, with a colorless basal globule, apparently emerging through pores formed upon the deliquescence of the two opposite papillae (rarely, also, a third, apical, papilla); resting spore sessile, subspherical or spherical, outer wall smooth, yellowish, inner wall colorless, contents with from one to two large globules, upon germination forming zoospores which escape through an apical pore.

On actively motile cells of *Chlamydomonas pulvisculus*, also possibly on *C. obtusa*, *Gonium tetras*, Braun (*loc. cit.*), GERMANY; *Chlamydomonas pulvisculus*, *Hormiscia* sp., de Wildeman (1890:15; 1894:156), BELGIUM; *Chlamydomonas Dillii*, Dangeard (1900-1901e:282, figs. A-L), FRANCE.

Braun noted that the swarmers were attacked by the chytrid zoospores, up to twelve parasites being formed on a single host cell. Eventually infected swarmers came to rest and were killed by the fungus. Dangeard observed the penetration of the alga by the slender germ tube of the fungus, but was unable to determine whether or not this tube remained unbranched during the subsequent development of the parasite. Eventually the contents of the alga were reduced to an amorphous reddish mass. Dangeard's resting spores were said to be spherical, but in the figures appear rather subspherical.

Several other species of *Rhizophydium* have been found to possess the peculiarly shaped sporangia characteristic of this species. *R. goniosporum* differs in having polygonal resting spores, sexually formed. *R. irregulare* (de Wildeman) Fischer appears only doubtfully distinct by reason of a difference in substratum (diatoms).

The sporangia of the fungus identified with this species by Cook (1932a:136, figs. 20-25) are too spherical for it to be *Rhizophydium transversum*. It may possibly be *R. acuforme*.

RHIZOPHYDIUM IRREGULARE (de Wild.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):105. 1892

Phlyctidium irregulare de Wildeman, Ann. Soc. Belge Micro. (Mém.), 14:21. 1890.

Sporangium sessile, citriform or broadly ovoid, with two opposite lateral papillae (sometimes only one), about 12μ broad by $8-10 \mu$

high, the longer axis parallel with that of the host cell, wall colorless, smooth, somewhat thickened; endobiotic system not observed; zoospores not observed with certainty, presumably emerging through one or two pores formed upon the deliquescence of the papillae; resting spore epibiotic, strongly subspherical, $14-15 \mu$ in diameter by 12μ high, wall thick, smooth, contents without a prominent globule, rhizoidal system branching, germination not observed.

Parasitic on small diatoms, de Wildeman (*loc. cit.*), BELGIUM; *Hantzschia Amphioxys*, Scherffel (1925b:24, pl. 2, fig. 51), HUNGARY.

Scherffel, to whom we owe most of our knowledge of this species, points out that the peculiarly shaped "roll-like" sporangium is not characteristic of *Rhizophydium irregularare* alone, but is also found in *R. transversum* and *R. gonioporum*. The species is only doubtfully distinct from *R. transversum*, the chief difference being that of substratum. The angular sexually formed resting spore of *R. gonioporum* differentiates it.

If the rhizoidal system attached to the sporangium should prove to be unbranched rather than branched, as it is on the resting spores, de Wildeman's binomial would be the more correct one.

RHIZOPHYDIUM GONIOSPORUM Scherffel

Arch. Protistenk., 53:20, pl. 1, figs. 40-42, pl. 2, figs. 43-50. 1925

(Figure 11 U-V, p. 164)

Sporangium sessile, broadly citriform or broadly ovoid, occasionally irregular, with a slightly flattened upper surface, its long axis parallel with that of the host filament, $5-11 \mu$ high by $7-16 \mu$ broad, with two lateral opposite papillae (rarely one), wall thin, smooth, colorless; rhizoidal system delicate, branched; zoospores ovoid or somewhat rodlike, $3-6 \mu$ long by $2-3 \mu$ in diameter, with an eccentric colorless globule and a short flagellum, escaping amoeboidly through one or two pores formed upon the deliquescence of the papillae, movement a brisk gliding; resting spore sessile, polyhedral, six- to eight-cornered in optical section, the corners often somewhat protruding, $6-7 \mu$ in breadth, wall thick, colorless, contents with few to many refractive globules, endobiotic part consisting of a central, possibly branched, axis, germination not observed; companion cells one or two, spherical or ovoid, 3μ in diameter, wall thin, smooth, colorless, attached directly to the receptive thallus (resting spore),

into which its contents are discharged and from which after fertilization it is separated by a cross wall.

Parasitic on *Tribonema bombycinum*, Scherffel (*loc. cit.*), HUNGARY; Sparrow (1936a:439, fig. 2 a-j), ENGLAND; Sparrow, UNITED STATES (MICHIGAN).

As pointed out by Scherffel, the sporangia of this species are like those of *Rhizophyllum transversum* found on members of the *Volvocales* and of *R. irregulare* on *Hantzschia* and other diatoms. The angular resting spore, formed after a sexual process, and the host distinguish *R. gomiosporum* from both these species.

Scherffel noted that the parasite formed rose-red products of decomposition in the host cell. These were not observed by Sparrow. The American material differed from Scherffel's in having smaller zoospores ($3 \times 2 \mu$ compared with $6 \times 3 \mu$), which bore an anterior rather than a basal globule.

SECTION V¹

RHIZOPHYDIUM MESSANENSE Morini

Malpighia, 10:79, pl. 3, figs. 1-4. 1896

(Figure 11 Y, p. 164)

Phlyctochytrium messanense (Morini) Minden, Kryptogamenfl. Mark Brandenburg, 5:339. 1911 (1915).

Sporangium narrowly ellipsoidal to cylindrical, $48-54 \mu$ high by $17-22 \mu$ in diameter, wall thin, smooth, colorless; rhizoids branched, arising from a stout main axis which is slightly expanded just beneath the host wall; zoospores spherical, pale rose-colored, $3.25-4 \mu$ in diameter, with an oil globule, escaping through a wide apical pore; resting spore spherical, $21-31 \mu$ in diameter, with a thick smooth brownish-red exospore, forming zoospores upon germination.

In *Cladophora*, ITALY.

There is little reason for considering the slight inflation of the subsporangial part of the main rhizoidal axis to be of sufficient import to warrant transference of the species to *Phlyctochytrium*. From the figure, the resting spore upon germination appears to have cracked open and emitted the spores through a wide aperture.

¹ See also the following imperfectly known species of *Rhizophyllum*: *R. Coleochaetes*, p. 217; *R. Hormidii*, p. 217.

RHIZOPHYDIUM FUSUS (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):99. 1892
(Figure 11 X, p. 164)

Rhizidium fusus Zopf, Nova Acta Acad. Leop.-Carol., 47:199, pl. 18,
figs. 9-12. 1884.

Sporangium sessile or borne on a short stalk, narrowly to broadly fusiform, usually slightly tilted, 10.4-20 μ high by 3-8 μ in diameter in mid-region, wall thin, smooth, colorless; rhizoids extensive, much branched, monophagous or polyphagous, arising from a relatively stout central axis; zoospores spherical, 2-2.5 μ in diameter with a colorless globule and a flagellum, emerging through a small apical often slightly protruding pore; resting spore not observed.

Parasitic on *Synedra* sp., Zopf (*loc. cit.*), GERMANY; various diatoms, de Wildeman (1890:12), BELGIUM; *Melosira*, de Wildeman (1894:156), FRANCE; *Cymbella*, *Gomphonema constrictum*, Scherffel (1902a:[106]), HUNGARY; *Melosira varians*, Sparrow (1932b:276, text fig. 2 a-b; 1933c:519), UNITED STATES; *Surirella* sp., *Pinnularia* sp., Tokunaga (1934b:389, pl. 11, fig. 4), JAPAN; *Melosira varians*, Sparrow (as *Rhizophydiwm Lagenula*, 1936a:439, fig. 4 k-m), ENGLAND; *Synedra* sp. (coll. P. W. Richards), Sparrow (1938a:148, fig. 2d), SARAWAK.

Doubt exists as to whether or not Zopf's species is identical with Braun's *Chytridium Lagenula* on *Melosira* (Braun, 1856a:31, pl. 2, figs. 2-3). Scherffel (see *C. Lagenula*, p. 336) believes that two distinct fungi were grouped under this name by Braun, one occurring on *Melosira*, the other on *Tribonema*. Since the rhizoids were not observed by Braun in either form, it is difficult to attempt an analysis of his species. Zopf's specific name is preferred for the diatom parasite because it has been applied to a more completely known organism.

The fungus is parasitic and, as Zopf noted, the nucleus and plasma of the host cells are consumed, leaving only an olive-green or brownish residue of chloroplast material. On *Melosira* the rhizoids may ramify through from five to six cells of the host.

Cejp (1933a:4, pl. 1, fig. 11) has described as *Rhizophydiwm Lagenula* (Braun) Fischer an organism on *Mougeotia* that agrees with *R. fusus* in the fusiform shape of the sporangium, but which is larger (30 μ or more long by 8-10 μ in diameter) and which forms epibiotic spherical thick-walled resting spores 25 μ in diameter. He considers *R. Lagenula* to be identical with *R. fusus*.

RHIZOPHYDIUM GIBBOSUM (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):102. 1892

(Figure 11 W, p. 164)

Rhizophyton gibbosum Zopf, Nova Acta Acad. Leop.-Carol., 52:344, pl. 20, figs. 8-20. 1888.

Sporangium sessile, ovoid, pyriform, or fusiform in outline, with several or many humplike lobes which give an irregular gibbose appearance to the whole structure, sporangia, when few on a cell, up to 25-45 μ long by 10-20 μ in diameter, when many, 11 μ long by 8 μ in diameter, upright or somewhat tilted, with a single terminal broad papilla, wall colorless, fairly stout; rhizoids profusely branched, arising from a main axis, which is occasionally slightly swollen; zoospores spherical, small, 2.5-3.9 μ in diameter, with a delicate flagellum and a few small colorless globules, escaping upon the deliquescence of the papilla; resting spore not observed.

Parasitic on *Penium*, *Cylindrocystis*, *Phycastrum*, palmellaceans, pinnularians, rotifer eggs, Zopf (*loc. cit.*), GERMANY; rotifer eggs, Scherffel (1904:116), HUNGARY; *Navicula* *sp.*, Sparrow (1933c:519, pl. 49, fig. 13), UNITED STATES.

On desmids the sporangia were generally collected in groups at the isthmus of the cell. Rotifer eggs soon died after being attacked, their contents eventually being nearly completely absorbed by the fungus.

The species is of interest because of its ability to live on a variety of substrata. Since the sporangium possesses so distinctive a configuration there is little question but that the same organism is involved in all instances.

IMPERFECTLY KNOWN SPECIES OF RHIZOPHYDIUM

SECTION I

On Fresh-Water Algae

? RHIZOPHYDIUM CAUDATUM (Reinsch) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:38. 1896

Olpidium caudatum Reinsch, J. Linn. Soc. London (Bot.), 15:215. 1877.*Sphaerostyliidium caudatum* (Reinsch) Berlese and de Toni, in Saccardo, *Sylloge fungorum*, 7:309. 1888.

Like *Rhizophydiumpampullaceum*, but larger (12–13 μ in diameter) and with thicker walls.

On *Schizosiphon kerguelensis*, coll. Eaton, KERGUELEN ISLANDS.

? *RHIZOPHYDIUM DECIPIENS* (Braun) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):100. 1892

Chytridium decipiens Braun, Monatsber. Berlin Akad., 1855:383; Abhandl. Berlin Akad., 1855:54, pl. 5, figs. 1–4. 1856.

Phlyctidium decipiens (Braun) Cornu, Ann. Sci. Nat. Bot., V, 15:121. 1872.

Olpidiella decipiens (Braun) Lagerheim, Journ. de Botanique, 2:439. 1888.

Olpidium (?) *decipiens* (Braun) H. E. Petersen, Bot. Tidsskrift, 29:423, fig. 25f. 1909; Ann. Mycologici, 8:555, fig. 25f. 1910.

Sporangium within the oögonium of the alga but resting on the surface of the oöplasm, spherical, subspherical, ovoid, or, if several sporangia in a cell, occasionally somewhat irregularly tubular, variable in size, up to 41 μ in diameter, wall smooth, colorless, thin or slightly thickened, discharge tube broad, short-cylindrical or only slightly elevated, its apex protruding through the oögonial pore; rhizoids not observed; zoospores numerous, spherical or slightly elongate, 2.5–4 μ in diameter, with a colorless, eccentric globule and a long flagellum, movement hopping or amoeboid; resting spore resting in the oögonium, apparently without rhizoids, ovoid or somewhat angular, rarely spheroidal, 18–36 \times 20–39 μ , wall very thick (2–6 μ), colorless, often showing radial striations, contents evenly granular, without a large globule, germination not observed.

In oögonia of *Oedogonium echinospermum*, *O. tumidulum*, Braun (*loc. cit.*), *O. Vaucherii* (coll. Pringsheim), Braun (*loc. cit.*), GERMANY; *Oedogonium* sp., Cornu (1872a:121), FRANCE; *Oedogonium* sp.; Sorokin (1883:26, fig. 26), EUROPEAN RUSSIA, ASIATIC RUSSIA; *Oedogonium* sp., de Wildeman (1893b:59, pl. 7, figs. 5–11), BELGIUM; (coll. Pittier) de Wildeman (*loc. cit.*), COSTA RICA; *Oedogonium* sp., Petersen (1909:423; 1910:555, fig. 25f), DENMARK; *Oedogonium Vaucherii*, *O. cardiacum*, *O. sexangulare*, *O. rufescens*, Scherffel (1926a:219, pl. 10, figs. 98–102), HUNGARY.

It is debatable whether or not this is a species of *Rhizophydiumpampullaceum*. As Petersen (*loc. cit.*) points out, no rhizoids have ever been found.

Scherffel, however, who has made the most critical study of it, emphasizes the fact, pointed out by Braun, that the sporangium is "extramatrical" and rests on the egg cell, which in turn is surrounded by the oögonial wall. He further states that even if a rhizoidal system were definitely shown not to be present in the dense host plasma he could not consider it a species of *Olpidium* since the discharge tube does not penetrate the host wall. Further observations, particularly on stained material, will be necessary before this fungus can without doubt be referred to *Olpidium*, *Rhizophydiuum*, or, possibly, to *Entophysycis*.

Braun (1856a) records the remarkable fact that the zoospores of the species which remained in the sporangium swarmed for as much as 108 hours. Sorokin (*loc. cit.*) describes them as being actively motile after 48 hours.

? *RHIZOPHYDIUM DIGITATUM* Scherffel

Arch. Protistenk., 54:223, pl. 10, figs. 103-104. 1926

Sporangium single, somewhat broadly ovoid, with truncate apex, 8 μ in diameter, wall thin, smooth, colorless, bearing on the rim of the flattened top five coarse hollow thin-walled sharp somewhat incurved teeth 4 μ long by $\frac{1}{2}$ μ thick; rhizoid broad, somewhat swollen at place of attachment to the rounded base of the sporangium, thin-walled, prolonged into a coarse filament which penetrates the host cytoplasm, where it probably branches; zoospores and resting spores unknown.

On *Gloeocystis*, *Mougeotia* sp., HUNGARY.

A form with four teeth incompletely observed by Sparrow (1933c: 529, fig. I, 17) may be referable to this species.

? *RHIZOPHYDIUM DUBIUM* de Wildeman

Ann. Soc. Belge Micro. (Mém.), 19:113, pl. 3, figs. 26-28. 1895

Sporangium sessile, spherical, with a protruding apical papilla, wall thin, smooth, colorless; rhizoids branched, delicate, arising from a short central axis; zoospores not observed, apparently emerging through a wide pore formed upon the deliquescence of the papilla; resting spore not observed.

On filaments of *Spirogyra*, FRANCE.

? RHIZOPHYDIUM EPITHEMIAE Valkanov

Arch. Protistenk., 73:362, fig. 2. 1931

Sporangium sessile, spherical, up to 21 μ in diameter, colorless, with a prominent thick-walled subapical wartlike protrusion, wall otherwise thin, smooth; rhizoids fairly stout, short, branched, arising from a short main axis; zoospores not observed, apparently emerging through a fairly large lateral pore; resting spore not observed.

Parasitic on *Epithemia zebra*, BULGARIA.

The curious wartlike protrusion may possibly be the case of the infecting zoospore which, as in *Chytridium Schenkii*, has persisted.

? RHIZOPHYDIUM FALLAX Scherffel

Arch. Protistenk., 53:30, pl. 2, figs. 60-62. 1925

Sporangium sessile, spherical, variable in size, wall smooth, colorless, fairly thick; endobiotic part not distinctly observed, being surrounded by a large pale reddish-brown peglike thickening of the host wall; zoospores narrowly ovoid, with a colorless lateral oil globule and a short slowly moving posterior flagellum attached to the narrower end of the body, emerging individually through one (or more?) minute needle-like scarcely perceptible lateral pore, movement gliding or amoeboid, never hopping; resting spore epibiotic, sessile, spherical, 8-10 μ in diameter, with a smooth double wall 1 μ thick, contents with a large (8 μ in diameter) colorless eccentric globule or with from two to three globules, endobiotic part like that of the sporangium, germination not observed; companion cells one or two, smooth-walled, 3 μ in diameter, directly attached to the receptive thallus (resting spore), wall at first thin, later thickening.

On *Mougeotia sp.*, HUNGARY.

Differing from *Rhizophydiump globosum* in lacking a prominent exit pore and in having ovoid gliding spores and smooth colorless resting spores.

Further observations on the endobiotic system will be necessary to determine whether this is a species of *Rhizophydiump* or of *Phlyctidium*.

? RHIZOPHYDIUM HYALOTHECAE Scherffel

Arch. Protistenk., 54:201, pl. 9, fig. 64. 1926

Sporangium borne at the tip of a narrowly clavate extramatrical stalk, imbedded, with the exception of its apex, in the gelatinous sheath of the host, ovoid, 23μ high by 22μ in diameter, apex somewhat flattened, bearing a crown of prominent solid somewhat incurved plain long (2μ) teeth (undetermined number), wall smooth, somewhat thick, colorless; endobiotic system not observed; zoospores spherical, with an eccentric colorless globule and a single flagellum, discharge not seen; resting spore not observed.

On *Hyalotheca dissiliens*, HUNGARY.

Further observations on the number of teeth and the nature of the endobiotic system are needed before the species can be adequately defined.

? RHIZOPHYDIUM v. MINDENI Valkanov

Arch. Protistenk., 73:363, figs. 6-8. 1931

Sporangium spherical, with from twenty to thirty long delicate hairs radiating from the upper part, discharging its spores by means of a terminal splitting; otherwise unknown.

On oögonia of *Oedogonium sp.*, BULGARIA.

Probably referable to *Chytridium chaetophilum* or *Rhizophydiuum chaetiferum*.

? RHIZOPHYDIUM MULTIPORUM de Wildeman

Mém. Herb. Boissier, 1900 (15):7; Bull. Acad. Roy. Belg. (Sci.), V, 17:287, fig. 2. 1931

Sporangium sessile, spherical, subspherical, or somewhat ovoid, $32-52 \mu$ in diameter, with three or more prominent somewhat tubular papillae about 4μ in diameter, wall smooth; rhizoids, zoospores, and resting spore not observed.

Parasitic on oögonia of *Vaucheria sessilis*, coll. Massart, BELGIUM.

The fungus was never found on the vegetative filaments of the alga. It could not be induced to live on the pollen of *Salix* or *Alnus*.

Distinguishable from other multiporous species of the genus by the prominent discharge tubes.

? RHIZOPHYDIUM OEDOGONII Richter

Bibliotheca Botan., 42:12, fig. 6. 1897

Sporangia in groups, sessile, somewhat irregularly ellipsoidal with outgrowths which result in a spherical-tetrahedral shape, at maturity bearing two lateral opposite spines, breadth from spine to spine 28μ , thickness $14-17 \mu$; other features not observed.

On filaments of *Oedogonium sp.* (preserved material), GREENLAND.

? RHIZOPHYDIUM SPOROCTONUM (Braun) Berlese and de Toni

Saccardo, Sylloge fungorum, 7:299. 1888; emend. Scherffel, Arch. Protistenk., 54:222, pl. 10, figs. 96-97. 1926

Chytridium sporoctonum Braun, Monatsber. Berlin Akad., 1855:381; Abhandl. Berlin Akad., 1855:39, pl. 2, fig. 13. 1856.

Sporangium sessile, spherical, 7μ in diameter, wall smooth, thin; rhizoids not seen; zoospores not observed, liberated through a broad apical pore; resting spore (?) epibiotic, spherical, $15-19 \mu$ in diameter, with a very thick (4μ), pale ocher-yellow wall of two layers, outer wall 2.5μ thick in surface view, covered with raised punctations, appearing prismatic in optical section, inner wall 1.5μ thick, strongly refractive, homogeneous; germination not seen.

On oögonia of *Oedogonium Vaucherii*, Braun (*loc. cit.*), GERMANY; *Oedogonium Vaucherii* in company with *Chytridium olla*, Scherffel (*loc. cit.*), HUNGARY.

Fischer and others have regarded this species as being only the immature sporangia of a *Rhizophydiump*, possibly *R. globosum*. The small size of the empty sporangia found by Scherffel and the fact that his fungus occurred on the same host as Braun's have led him to suggest the reëstablishment of the species. Unfortunately, the lack of information on the exact nature of spore discharge and on the rhizoids, and want of positive proof other than association that the resting spores (observed by him) and sporangial stage belong to the same fungus make this suggestion of questionable value.

On Marine Algae

? RHIZOPHYDIUM DISCINCTUM H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):484,
fig. XI, 1-3

Sporangium sessile, at first spherical or subspherical, becoming somewhat angular with the formation at maturity of one or two subapical or lateral papillae, 8-30 μ in diameter, resting on a broad base, wall smooth, colorless, thick (1-2 μ or more); endobiotic part consisting of a stout unbranched (?) tube; zoospores 1-5 μ in length, method of discharge and flagella not observed; resting spore not observed.

On *Spongomorpha vernalis*, H. E. Petersen (*loc. cit.*), DENMARK; *Acrosiphonia incurva* (coll. F. Börgesen), H. E. Petersen (*loc. cit.*), NORWAY; *Ceramium diaphanum*, Sparrow (1936b:257, figs. 29-30), UNITED STATES.

Petersen distinguished sporangia of two sizes: ones 8-15 μ in diameter on *Spongomorpha*, and ones up to 30 μ in diameter on *Acrosiphonia*. Observations on the escape and flagellation of the zoospores and on the nature of the endobiotic part are needed to confirm the correctness of the present generic disposition of the species.

The fungus termed *Rhizophydiumpolysiphoniae* (Cohn) Petersen by Martin (1922:236, figs. 1-10) may, because of its thick wall and somewhat angular sporangia, possibly be referred to *R. discinctum*. Martin's fungus, however, possessed a relatively extensive branched rhizoidal system. If this had been present in *R. discinctum* it seems probable that the two observers would have seen it.

Sparrow considered that his fungus, which appeared on *Ceramium* maintained in a laboratory aquarium for a week, was only weakly if at all parasitic.

? RHIZOPHYDIUM GELATINOSUM Lind

Ann. Mycologici, 3:427, 3 figs. (p. 427). 1905

Sporangium sessile, spherical, 20-30 μ in diameter, with a short stalklike base, wall thin, smooth, colorless, surrounded by a gelatinous hull about 3 μ thick; rhizoids not observed; zoospores not

observed, apparently escaping through eight sessile pores 4–6 μ in diameter formed on the upper surface of the sporangium; resting spore not observed.

On *Acrosiphonia (Cladophora) pallida*, coll. Svedelius, SWEDEN.

The organism is remarkable for the number of pores formed and for the thick gelatinous sheath which surrounds the sporangia. That the structure is fungoid at all is doubtful.

? RHIZOPHYDIUM MARINUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 17:11. 1893

Sporangium sessile, spherical, 7–15 μ in diameter, wall smooth, colorless; rhizoids few; zoospores and resting spore not observed.

On *Melosira* sp., in marine aquarium, BELGIUM.

Possibly a marine form of the "*Rhizophydium globosum*" type, as are those mentioned by Sparrow (1936b:258).

On Aquatic Phycomycetes

? RHIZOPHYDIUM PARASITANS Scherffel

Arch. Protistenk., 53:26, pl. 2, figs. 52–56. 1925

Sporangium sessile, spherical, 8–10 μ in diameter, with a thin smooth colorless wall; endobiotic part not observed; zoospores spherical, mostly 4 μ in diameter, with a colorless eccentric globule and a posterior flagellum about 24 μ in length, emerging through a wide pore at the apex of the sporangium and either forming a compact motionless group at the orifice before dispersing or escaping individually and amoeboidly, in either case assuming suddenly a lively hopping movement; resting spore sessile, spherical, 6 μ in diameter, with a thick smooth colorless wall, the outer margin dark and sharply defined, contents coarsely granular, with an eccentric colorless fat globule, 2 μ in diameter, germination not observed.

Parasitic on sporangia of *Rhizophydium goniosporum* parasitizing *Tribonema bombycinum*, HUNGARY.

A curious condition of hyperparasitism is shown by this species. Scherffel noted that certain sporangia of *Rhizophydium goniosporum* had within them a spherical thick-walled resting structure or "cyst" of uncertain origin. The sporangia of *R. parasitans* were found only on sporangia of *R. goniosporum* which contained the remains of these

cysts. Against the hypothesis proposed by Scherffel, namely, that the epibiotic sporangia of *R. parasitans* were in reality sporangia formed by germination of the endogenous cysts, was the fact that epibiotic resting spores also occurred on *R. goniosporum*. These were never found, however, on sporangia bearing the endogenous parasite. If these facts present the correct interpretation of the structures observed by Scherffel, then the sporangial stage of the species is parasitic on the encysted stage of an unidentified organism, possibly a monad, which in turn has parasitized the sporangium of *R. goniosporum*, which in turn has parasitized the alga *Tribonema*. The resting stage of *R. parasitans*, on the other hand, is directly parasitic on the sporangium of *R. goniosporum*, or—a possibility not mentioned by Scherffel—on the feeding or “vegetative” stage of the extraneous, cyst-forming, organism.

Further observations, particularly on the nature of the endobiotic system and on just what structure is penetrated by the zoospore of *Rhizophydiuum parasitans*, will be necessary before this puzzle can be solved with certainty.

On Microscopic Animals

? *RHIZOPHYDIUM CHRYSOPYXIDIS* Scherffel

Arch. Protistenk., 54:174, pl. 9, fig. 12. 1926

Sporangium sessile, ovoid, 8 μ long by 6 μ in diameter, with a prolonged apical beak and a narrow base, wall thin, smooth, colorless; endobiotic part consisting of a short fairly thick unbranched tube which terminates in a knob-shaped swelling; zoospores and resting spore not observed.

Attached to the mid-region or under part of the lorica of *Chrysopyxis* sp., HUNGARY.

Possibly a species of *Phlyctidium*.

On Unknown Substratum

? *RHIZOPHYDIUM TRANZSCHELII* Jaczewski

Opredelitel gribov.... I. Fikomitsety, p. 39. 1931

Sporangium spherical, 39 μ in diameter, with a single opening; zoospores 4–5 μ long; resting spore spherical, 15 μ in diameter.

RUSSIA.

SECTION II

On Fresh-Water Algae

? RHIZOPHYDIUM (?) PERSIMILIS Scherffel

Arch. Protistenk., 54:199, pl. 9, figs. 60-61. 1926

Sporangium sessile, broadly pyriform, with a broad flat-arched somewhat conical apex, 20-24 μ high by 15-16.6 μ in diameter, wall rather thick, smooth, colorless; endobiotic part not observed; zoospores and method of sporangial discharge not observed; resting spore (?) sessile, spherical, 8-12 μ in diameter, with a somewhat thickened wall covered on its outer surface with small wartlike granulations, contents with a large eccentric oil globule, germination not observed; male cell spherical, 4-6 μ in diameter, wall smooth, thick, attached laterally to the receptive thallus (resting spore).

On Tribonema bombycina, HUNGARY.

As Scherffel suggests, the resting spore is very much like that formed by *Rhizophydiump granulosporum*. The sporangia of the latter are, however, distinctly smaller than those associated with the present species. Endogenous cysts belonging to an unknown parasitic organism were found in the sporangia.

? RHIZOPHYDIUM PYRIFORMIS Valkanov

Arch. Protistenk., 73:362, figs. 3-5. 1931

Sporangium sessile, narrowly pyriform with a broad rounded apex, broadly obpyriform or oblong with one constriction (rarely with two); rhizoids branched, arising from the base of a broad penetration tube; zoospores not observed, apparently escaping through a terminal opening; resting spore not observed.

Parasitic on ripe oospores of *Vaucheria sp.*, BULGARIA.

? RHIZOPHYDIUM SP. Karling

Bull Torrey Bot. Club, 65:451, pl. 21, figs. 18-33. 1938

"*Rhizophidium sp.* occurs saprophytically on a wide variety of dead filamentous and unicellular algae, flagellates, rhizopods, rotifers, liver fluke ova and ovarian tissue, eggs, larvae and exuviae of insects, cooked striated muscle cells and root tips of various plants. The

sporangia may be almost spherical ($10\text{--}52 \mu$), slightly depressed, wedge-shaped and somewhat triangular ($14 \times 29 \mu$ — $25 \times 30 \mu$), oval and occasionally slightly irregular with 1 to 11 exit papillae. The smaller sporangia may often resemble those of *R. agile*, *R. gibbosum*, *R. rostellatum* and *Phlyctochytrium bispororum* [*biporosum*]. Resting spores have so far not been found" (Karling, *loc. cit.*).

? *RHIZOPHYDIUM* SP. Scherffel

Arch. Protistenk., 53:28, pl. 2, figs. 57-59. 1925

Sporangium sessile, upright, pyriform, 8μ high by 5μ in diameter at the base, wall smooth, colorless; endobiotic system not observed; zoospores not observed; immature resting spore ovoid, with a flattened base, wall thin, smooth, colorless, contents homogeneous, with one or two large oil droplets, becoming spherical at maturity; contributing thalli from one to three, small, somewhat spherical or ovoid, attached directly or by a short copulation tube to the base of the receptive thallus; other characters unknown.

On *Tribonema bombycina*, HUNGARY.

Scherffel is not certain that the sporangial stage observed belonged to the fungus which was forming resting spores.

? *RHIZOPHYDIUM* SP.

Sporangium sessile, spherical, subspherical, or broadly urceolate, with an apical or subapical papilla, $5.5\text{--}10 \mu$ in diameter, wall smooth, thin, colorless; zoospores not observed, apparently emerging through a single somewhat broad apical or subapical pore; rhizoidal part consisting of a tuft of poorly developed digitations which arise from a short stout main axis; resting spore epibiotic, spherical, 10μ in diameter, with a thick smooth colorless wall, rhizoids consisting of a tuft of short digitations, germination not observed.

On *Bumilleria* sp., Couch (1932:252, pl. 17, figs. 84-87), UNITED STATES; *Spirogyra* sp., Sparrow (1936a:443, fig. 3s), ENGLAND.

Since the discharge of the zoospores has not been observed, the fungi of Couch and Sparrow may belong in *Chytridium*. The formation of epibiotic resting spores, however, makes this improbable. Though the sporangia of the American and British forms differ slightly in shape, the former being spherical or subspherical, the

latter more urceolate, they agree in being attached to the host cell by short digitate rhizoids. Couch states that the resting spore is surrounded by a gelatinous sheath. This has been interpreted in the British fungus as wall material.

Couch discussed his fungus under the name *Rhizophydiwm minium* (Schroeter) Fischer, but it differs markedly from that species and from other members of the genus in the character of its endobiotic system. Further study may possibly show the fungi on *Bumilleria* and *Spirogyra* to be distinct.

On Microscopic Animals

? *RHIZOPHYDIUM LEPTOPHYRDIS* Scherffel

Arch. Protistenk., 54:172, pl. 9, fig. 9. 1926

Sporangium sessile, very broadly pyriform, with a prominent broad conical subapical protrusion (papilla?), 24 μ high by 21 μ in diameter, the protrusion 10 μ in diameter at the base by 5 μ high, wall thin, smooth, colorless; rhizoidal system, zoospores, and resting spore not observed.

On the zoocyst of the vampyrellan *Leptophys vorax*, HUNGARY.

Differing from *Rhizophydiwm Vampyrella* (Dang.) Minden in having a pyriform rather than a spherical sporangium.

SECTION III

On Fresh-Water Algae

? *RHIZOPHYDIUM SEPTOCARPOIDES* H. E. Petersen

Bot. Tidsskrift, 29:420, fig. 24d. 1909; Ann. Mycologici, 8:552, fig. 24d. 1910

Sporangium resting on a short needle-like extramatrical stalk, obpyriform, 8-16 μ high, the basal part distinctly cylindrical, wall thin, smooth, colorless; rhizoids poorly developed, once branched, arising from a main axis which is continuous with the short extramatrical stalk; zoospores and resting spore not observed.

On *Closterium spp.*, DENMARK.

This incompletely known species resembles a small form of *Chytridium versatile*. Until spore discharge is described it cannot be

placed generically with any certainty. Sparrow (1936a:437, fig. 3t) has described a fungus on diatoms in England which resembles Petersen's species very closely in size and shape. Here again, however, no spore discharge was witnessed.

SECTION IV

On Fresh-Water Algae

? RHIZOPHYDIUM ASTEROSPORUM Scherffel

Arch. Protistenk., 53:17, pl. 1, figs. 30-39. 1925

Sporangium sessile, short cylindrical, pouchlike, or somewhat tubular, slightly curved and attenuated at one end, its long axis parallel or nearly so with that of the host filament, wall smooth, thin, colorless; endobiotic part not observed; zoospores (quiescent) spherical, with a small colorless globule, escaping through a broad pore formed at the narrower end of the sporangium; resting spore somewhat elongate and irregularly starlike, 12 μ long by 6-9 μ high, the outer surface of the thickened wall bearing prominent blunt conical solid refractive outgrowths 3 μ high by 3 μ broad at the base, contents with a few large or numerous smaller colorless oil globules, rhizoids (seen once) numerous, delicate; companion cell spherical, smooth-walled, 2 μ in diameter, directly attached at various points to the resting spore.

Parasitic on *Tribonema bombycinum*, HUNGARY.

The resting spore, as Scherffel points out, is shaped very much like the sporangium of the incompletely known *Chytridium cornutum* Braun on *Sphaerozyga*, a blue-green alga.

Only quiescent zoospores within the sporangium were observed by Scherffel.

? RHIZOPHYDIUM BARKERIANUM (Archer) Rabenhorst

Flora Europaea algarum, 3:281. 1868

Chytridium Barkerianum Archer, Quart. J. Micro. Sci. (N. S.), 7:89. 1867.

Sporangium sessile, strongly flattened, with a concave upper surface from the center of which arises a slender stalk terminating in a

small swelling, deeply three- to four-lobed, the lobes of equal size, with rounded apices and radiating in one plane; rhizoids, where observed, rootlike; zoospores escaping from the open ends of the lobes; resting spore not observed.

On *Zygnema* sp., IRELAND.

This curious species, said by its author to be related to *Rhizophy-
dium cornutum* and *R. transversum*, is of doubtful validity. The pecu-
liar central stalk terminating in a knob is difficult to interpret
unless it be the cyst of the zoospore. If so, the fungus would have a
type of development like that of the *Scherffeliomyces*.

? **RHIZOPHYDIUM SPIROTAENIAE** (Scherffel), comb. nov.

Chytridium (?) *Spirotaeniae* Scherffel, Arch. Protistenk., 53:14, pl. 1,
figs. 26-29. 1925.

Sporangium epibiotic, broadly ovoid, its longer axis parallel with that of the host cell, with a conical protuberance (papilla) eccentrically placed on the somewhat flattened upper surface, 12-14 μ in diameter by 8-9 μ high, wall smooth, colorless, thin, opening with an apical or lateral pore; rhizoids not observed; resting spore epibiotic, sessile (?), colorless, spherical, 11-20 μ (generally 16 μ) in diameter, wall of two layers, the outer densely covered with broad, blunt or pointed, straight or slightly curved, solid, refractive, raylike protuberances 3 μ wide at the base by 2-3 μ high, inner wall smooth, 2 μ thick, contents colorless, with numerous coarse globules (fat?), germination not observed; male cell epibiotic, sessile (always?), rounded, smooth, thin-walled, apparently without rhizoids, connected to the resting spore by a cylindrical tube 2 μ in diameter which is expanded distally to form a spherical or pyriform swelling, the tubular part sometimes lacking.

Parasitic on *Spirotaenia condensata*, HUNGARY.

Because of the lack of data on the rhizoids and the type of discharge the fungus cannot yet be accurately placed generically. Scherffel suggests that it is a species of either *Zygorhizidium* or *Rhizophy-
dium*, depending on whether it is operculate or inoperculate. It is here considered to belong to the latter genus because of the epibiotic resting spore and the shape of the sporangium.

SECTION V

On Fresh-Water Algae

? RHIZOPHYDIUM COLEOCHAETES (Nowak.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):99. 1892

Chytridium Coleochaetes Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2:80, pl. 4, figs. 5-10. 1876.*Olpidium Coleochaetes* (Nowakowski) Schroeter, Kryptogamenfl. Schlesien, 3 (1):182. 1885.

Sporangium resting on the surface of the egg of the host but elongating within, filling the trichogyne and extending and expanding beyond it, terminating distally in a short tubular portion with a blunt rounded apex, the whole body thus being unequally spindle-shaped, up to 125μ in length (average 80μ) by 12μ in greatest diameter, wall thin, smooth, colorless; rhizoids not observed; zoospores small, spherical, 2μ in diameter, with a minute colorless refractive globule and a flagellum, emerging through a pore formed at the apex of the sporangium; resting spore not observed.

Parasitic on oögonia of *Coleochaete pulvinata*, GERMANY.

The zoospore gains access to the oögonium by swimming down the open trichogyne. The developing fungi, of which as many as four attack a single egg, then consume the entire contents of the oöospheres, leaving only a small amount of reddish-brown residue.

Whether or not this is a species of *Olpidium*, as Schroeter has supposed, depends upon the interpretation of the position of the sporangium and the possible absence of rhizoids. Fischer and Minden consider the body of the fungus to be extramatrical in the already opened oögonium. The apparent lack of a rhizoidal system even in nearly empty oögonia, however, appears to strengthen Schroeter's interpretation. New observations will be necessary before a final generic disposition can be made.

? RHIZOPHYDIUM HORMIDI^{II} Skvortzow

Arch. Protistenk., 51:480, text fig. 5. 1925

Sporangium narrowly clavate or curved and fusiform, $5.7-7 \mu$ long by $1.5-2 \mu$ in diameter, wall thin, smooth, colorless; rhizoids

delicate; zoospores one or two, 1μ in diameter, with an oil droplet and a single flagellum; resting spore not observed.

On *Hormidium flaccidum*, *Mougeotia viridis*, MANCHURIA.

Neither the description nor the figures are adequate enough to characterize this species properly.

REJECTED SPECIES OF RHIZOPHYDIUM

* *RHIZOPHYDIUM MICROSPORUM* (Nowak.) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):97. 1892

Chytridium microsporum Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2:81, pl. 4, fig. 11. 1876.

Phlyctidium microsporum (Nowak.) Schroeter, Kryptogamenfl. Schlesien, 3 (1):190. 1885.

Sporangium sessile, more or less spherical or ovoid, 30–50 μ in diameter, wall thin, colorless; rhizoids not observed; zoospores minute, somewhat elongate with a narrower anterior end, 2μ long by $\frac{2}{3} \mu$ wide, with a strongly refractive anterior granule and a single fairly strong anterior flagellum, emerging in great numbers from an imperceptible orifice and quickly swimming away; resting spores not observed.

On filaments of *Mastigothrix aeruginosa*, imbedded in the gelatinous sphere of *Chaetophora*, GERMANY.

From the anterior flagellation of the zoospore, the fungus belongs to none of the three genera to which it has been assigned. If further study confirms the observations of Nowakowski on this point it should be segregated in a new genus, and placed in the Hypochytriaceae.

* *RHIZOPHYDIUM MONOPORUM* Maire

Bull. Soc. Linn. Normandie, VI, 2:68. 1910

Sporangium opening by a single pore; rhizoids absent.

On pollen grains of *Pinus*, FRANCE.

Insufficiently described.

*** RHIZOPHYDIUM (?) SETIGERUM Scherffel**

Arch. Protistenk., 53:48, pl. 2, fig. 95. 1925

Resting spore sessile, spherical, thick-walled, the upper part of the outer wall with a tuft of long radiating hairs; other features unknown.

On oöspore of *Oedogonium sp.*, HUNGARY.

It is impossible to place this structure in any of the genera of the chytrids. It closely resembles the resting spore of *Rhizophydiump chaetiferum*.

*** RHIZOPHYDIUM UTRICULUS Scherffel**

Arch. Protistenk., 54:173, pl. 9, fig. 11. 1926

Sporangium sessile, consisting of an irregular more or less cylindrical short tube resting with its smaller, somewhat curved base on the substratum, 13–14 μ long by 6–8 μ in diameter, wall thin, smooth, colorless; endobiotic part not observed; zoospores not observed, apparently emerging through the broad open apex; resting spore not observed.

On cyst (?) of an unidentified chrysomonad, HUNGARY.

The description of the species is lacking in too many essential features for the fungus to be placed anywhere generically.

DANGEARDIA B. SCHRÖDER

Berichte Deutsch. Bot. Gesell., 16:321. 1898

(Figure 10 C–E, p. 152)

Thallus intramatrical, epi- and endobiotic, monocentric, eucarpic, consisting of the rudiment of the sporangium, which is sessile on the host contents but imbedded, except for its apex, in the gelatinous sheath of the host, and a complex of short bushy unbranched rhizoids; sporangium inoperculate, zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium, liberated through an apical pore; resting spore endobiotic, with a thick spiny or warty wall, formed at the tip of a fusiform persistent germ tube, germination not observed.

A monotypic genus known only as a parasite in members of the Volvocales.

Aberrant in forming an endobiotic resting spore and an epibiotic inoperculate sporangium, which is imbedded, save for its tip, in the gelatinous sheath of the host.

DANGEARDIA MAMMILLATA B. Schröder

Berichte Deutsch. Bot. Gesell., 16:321, pl. 20, figs. 1-14. 1898

Sporangium flask-shaped or pyriform, with a somewhat prolonged apex, 30μ long by $16-20 \mu$ in diameter, wall smooth, colorless, slightly thickened; rhizoids unbranched, short, bushy; zoospores ovoid to ellipsoidal, 3.4μ long by 2.5μ wide, with a flagellum from three to four times as long as the body and a large eccentric colorless refractive globule, resting for a short time at the orifice before assuming motility, movement hopping; resting spore ellipsoidal, with a thick spiny to papillate wall, 13.6μ long by 10.2μ broad, contents with a large eccentric globule.

Parasitic in nonsexual colonies of *Pandorina morum*,¹ Schröder (*loc. cit.*), GERMANY; Bartsch (communication), UNITED STATES; *Eudorina elegans*, Ingold (1940:102), ENGLAND.

Skvortzow (1927:206, figs. 5-8) has reported this fungus from Manchuria. Neither the bushy rhizoids nor the resting spore were observed, and hence the organism may be referable to *Rhizophydiaceae*.

PHLYCTOCHYTRIUM SCHROETER

Engler and Prantl, Natürlichen Pflanzenfam., 1 (1):78. 1892 (1893)
(Figure 10 H-I, p. 152)

Phlyctidium (Braun) Rabenhorst, Flora Europaea algarum, 3:278. 1868; Schroeter, pro parte, Kryptogamenfl. Schlesien, 3 (1):190. 1885.

Rhizidium sensu Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4):106. 1892. Non Braun, Monatsber. Berlin Akad., 1856:591.

Thallus epi- and endobiotic, monocentric, eucarpic, consisting of the epibiotic rudiment of the sporangium, the endobiotic apophysis,

¹ According to Miss Hood (1910), the host figured is *Eudorina elegans*.

and the branched rhizoidal system; sporangium inoperculate, epibiotic, uni- or multiporous, separated by a cross wall from the endobiotic system, zoospores posteriorly uniflagellate, generally with a single globule, formed within the sporangium; resting spore borne like the sporangium, thick-walled, apparently asexually produced, upon germination forming a zoosporangium.

Primarily parasites and saprophytes in fresh-water algae. Less often found in rotting parts of higher plants and occurring in one species (*Phlyctochytrium Synchytrii*) on the spores of another chytrid (*Synchytrium*).

The method of infection, establishment of the rhizoids, and formation of the apophysis are essentially as found in *Entophyscystis* except that the epibiotic part persists, receives the contents of the endobiotic system, and becomes the sporangium. Apophysate species of *Chytridium*, as for example *C. Lagenaria*, exhibit the same sequence of development as does *Phlyctochytrium*, but have never been segregated from *Chytridium* as have the inoperculate forms from *Rhizophydiuum*. This separation of apophysate from non-apophysate species has in most instances been readily accomplished. In several, however, the subsporangial swelling is not always definite, and in at least one (*P. biporosum*) it appears to be inconstant in its occurrence.

KEY TO THE SPECIES OF PHLYCTOCHYTRIUM¹

Sporangium wall smooth, not ornamented

Sporangium with a single apical discharge papilla

Sporangium spherical, subspherical, ovoid, pyriform, or dome-like, sessile, apophysis with or without rhizoids

Sporangium predominantly short-ovoid or pyriform, apophysis spherical, apparently without rhizoids²

P. Hydrodictyi, p. 223

Sporangium predominantly spherical, subspherical, or ovoid, with a blunt rounded apex, apophysis always bearing rhizoids

¹ See also the very recently published *Phlyctochytrium Lippsii* Lohman (*Mycologia*, 34: 104-111, figs. 1-15. 1942) and *P. proliferum* Ingold (*Trans. Brit. Mycol. Soc.*, 25: 45. 1941) on *Chlamydomonas*.

² Further observations will probably show that rhizoids are formed.

- Sporangium spherical
 - Sporangium 5-7 μ in diameter, with an apophysis of the same size; rhizoids delicate *P. equale*, p. 224
 - Sporangium 10-40 μ in diameter, apophysis much smaller than the sporangium; rhizoids stout and extensive *P. Hallii*, p. 224
- Sporangium subspherical, ovoid, or domelike, apophysis expanded laterally or subspherical
 - Apophysis minute; on *Chlamydomonas* *P. vernale*, p. 225
 - Apophysis conspicuous; on other algae
 - Sporangium subspherical or ovoid, with a laterally expanded apophysis; rhizoids arising from a basal axis or from several places on the apophysis *P. Lagenaria*, p. 225
 - Sporangium subspherical or domelike, with a subspherical apophysis; rhizoids arising from a single lateral main axis on the apophysis *P. laterale*, p. 226
 - Sporangium narrowly obpyriform, rarely ellipsoidal, sessile or on a slender stalk *P. Chaetophorae*, p. 227
- Sporangium with more than one discharge papilla
 - Sporangium spherical, up to 50 μ or more in diameter, with from one to nine protruding finger-like papillae, apophysis irregular, expanded against the host wall... *P. Synchytrii*, p. 227
 - Sporangium spherical or ovoid at first, forming two opposite apical papillae and becoming truncated and angular, apophysis only slightly expanded *P. biporusum*, p. 228
- Sporangium wall ornamented
 - Sporangium wall covered with long delicate flexible branching hairs *P. chaetiferum*, p. 229
 - Sporangium wall apically dentigerate
 - Teeth plain (not bipartite), four in number *P. planicorne*, p. 229
 - Teeth bipartite, variable in number or ten in a six-four arrangement
 - Teeth forming a single whorl around the discharge papilla
 - Sporangium spherical or broadly ovoid, teeth upright, shallowly cleft *P. Zyg nematis*, p. 230
 - Sporangium cylindrical or ovoid, teeth upright or converging, deeply cleft
 - Sporangium cylindrical or ovoid, teeth converging
 - P. dentatum*, p. 231
 - Sporangium broadly cylindrical or broadly ovate, with a rounded or flattened base, teeth upright
 - P. quadricorne*, p. 231

- Teeth forming two whorls around the papilla, the outer whorl
 containing six teeth, the inner, four
 Outer whorl of teeth borne at the top of large flangelike
 solid bosses, inner whorl sessile *P. bullatum*, p. 232
 Outer and inner whorls of teeth sessile
 Sporangium predominantly cylindrical and slightly ex-
 panded distally *P. urceolare*, p. 233
 Sporangium subspherical or ovoid *P. dentiferum*, p. 234

PHLYCTOCHYTRIUM HYDRODICTYI (Braun) Schroeter

Engler and Prantl, Natürlichen Pflanzenfam., 1(1):78. 1892 (1893)

- Chytridium Hydrodictyi* Braun, Monatsber. Berlin Akad., 1855:383;
 Abhandl. Berlin Akad., 1855:52, pl. 4, figs. 20-25. 1856.
Phlyctidium Hydrodictyi (Braun) Rabenhorst, Flora Europaea algarum,
 3:279. 1868.
Rhizidium Hydrodictyi (Braun) Fischer, Rabenhorst. Kryptogamen-Fl.,
 1 (4):108. 1892.

Sporangium sessile, short-ovoid or pyriform, with a rounded apex, 5-25 μ in diameter by 15-33 μ high, wall thin, smooth, colorless; endobiotic part consisting of a spherical subsporangial swelling about 5 μ in diameter, apparently without rhizoids; zoospores spherical, 3 μ in diameter, with a single globule, uniflagellate, escaping fully formed through an apical pore; resting spore not observed.

On diseased cells of *Hydrodictyon utriculatum*, Braun, Frantzius (in Braun, 1856a:53), Bail (1855:682), Rabenhorst (*loc. cit.*), GERMANY; *Hydrodictyon reticulatum*, de Wildeman (1891:171), BELGIUM; *Hydrodictyon reticulatum*, Valkanov (1931a:363), BULGARIA; *Rhizoclonium hieroglyphicum*, Sparrow (1932b:277, fig. 2c), UNITED STATES.

Presumably this is one of the first chytrids seen by Braun, in 1846 (Braun, 1856a:22). He describes the globules of the zoospores in the sporangium as yellowish or greenish yellow, a feature not mentioned by subsequent observers. Escape of the mature zoospores was observed by both Frantzius and Bail. The formation by the host of a protective plug of wall material at the point of entrance of the parasite was noted by Braun.

It is probable that further observations on this species will reveal the presence of rhizoids.

PHLYCTOCHYTRIUM EQUALE Atkinson

Bot. Gaz., 48:338, fig. 8. 1909

Sporangium sessile, spherical, $5\text{--}7 \mu$ in diameter, with a short apical discharge tube 1.5μ high by 2μ in diameter, wall thin, colorless; rhizoids delicate, branched, of limited extent, arising from the base of the spherical subsporangial apophysis, which is equal to the sporangium in diameter ($5\text{--}7 \mu$); zoospores not described; resting spore not observed.

Parasitic on *Spirogyra insignis*, Atkinson (*loc. cit.*), *S. Spreeiana*, Graff (1928:162), UNITED STATES.

Graff has pointed out that the toothlike projections described by Atkinson as being on either side of the exit pore are in reality the side walls of the short discharge tube viewed in optical section. He also states that there is no cross wall separating the endo- and epibiotic parts of the fungus and that the sporangium is not spherical but dumbbell-shaped, and neither wholly outside nor wholly inside the host. Further observations on this feature, which, incidentally, has also been noted by Schenk in *Phlyctochytrium Lagenaria*, are needed. Atkinson did not see zoospore discharge, and Graff describes it as occurring "in a manner typical for the genus."

PHLYCTOCHYTRIUM HALLII Couch

J. Elisha Mitchell Sci. Soc., 47:253, pl. 16, figs. 40-51. 1932

"Sporangia sessile, one to many on the host cell, often growing on the end of the cell; spherical, with a smooth rather thick wall; variable in size, when mature $10\text{--}40 \mu$ thick, usually $20\text{--}25 \mu$ thick. Sporangia with a bulbous base which may be as large as $5 \times 10 \mu$; bulbous base sometimes apparently absent. From the base a very conspicuous rhizoidal system arises. Spores formed as in *Rhizophidium*. Spores emerging through a large conspicuous pore, after which the spores slowly free themselves from the mass. The process of spore discharge strikingly resembles that of *R. sphaerocarpum* as figured by Zopf (1884). Spores $2.1\text{--}4.2 \mu$ thick, with a glistening droplet and one posteriorly directed cilium. Spores darting here and there with great rapidity. Resting cells thick-walled, bluntly spiny, with vesicle from which rhizoids arise, no small accompanying cell seen" (*Couch, loc. cit.*).

On *Spirogyra* sp., UNITED STATES.

During the process of infection the inner wall of the alga is depressed by the penetration tube. As development of the chytrid proceeds the chromatophores of the host lose their spiral arrangement and collapse toward the parasite. Eventually, the pyrenoids are broken up, the starch disappears, and the chloroplasts become bluish green and finally brown. Discharge of the zoospores regularly occurs in the late afternoon or early evening.

PHLYCTOCHYTRIUM VERNALE (Zopf) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:48. 1896

Rhizidium vernale Zopf, Nova Acta Acad. Leop.-Carol., 47:234, pl. 21, figs. 12-20. 1884.

Rhizophydiwm vernale (Zopf) Sparrow, Mycologia, 24:277, text fig. 2f. 1932.

Sporangium sessile, subspherical, with a slightly flattened apex, wall somewhat thickened, smooth, colorless; rhizoids coarse, sparingly branched, not extensive, arising from a main axis which is slightly expanded beneath the inner face of the host wall, forming a small apophysis; zoospores rather quickly formed, spherical, with a single prominent colorless globule and a flagellum, emerging through a fairly wide subapical slightly protruding pore; resting spore not observed.

Parasitic on *Chlamydomonas* sp., GERMANY.

No text and no sizes or magnification of the figures are given by Zopf. The first formal description of the species is found in Fischer (1892:108), derived, as is the present one, from the figures.

The fungus reported as *Rhizophydiwm vernale* on the zygospore of *Spirogyra* (Sparrow, 1932b:277, fig. 2f) possessed an apical or nearly apical papilla on the sporangium, which was 20-25 μ in diameter. Further observations are desirable before deciding finally whether or not it should be included in the present species of *Phlyctochytrium*.

PHLYCTOCHYTRIUM LAGENARIA (Schenk) Domján

Folia cryptogam., 2 (1):18, pl. 1, figs. 45-46, 48, 52-55, 62-63, 67, 69. 1936

Chytridium Lagenaria Schenk, pro parte, Verhandl. Phys.-Med. Gesell. Würzburg, A. F., 8:241, pl. 5, figs. 12, 14-15. 1858. Non *C. Lagenaria*

Schenk, Ueber das Vorkommen contractiler Zellen im Pflanzenreiche,
p. 5. Würzburg, 1858.

Sporangium sessile, subspherical, or ovoid, with a blunt rounded apex, $7.8-20 \mu$ in diameter (see discussion below), wall somewhat thickened, smooth, colorless, not giving a cellulose reaction; rhizoids unbranched or branched, arising from a single basal stalk or from several places on a subsporangial broadly expanded and flattened ($5.2-15.6 \mu$ wide by $5.2-11.2 \mu$ high) or spherical apophysis; zoospores ovoid, $2-5.2 \mu$ in diameter, with a colorless eccentric globule and a long flagellum, emerging through a broad apical pore; resting spore not observed.

On *Zygnema* sp., *Spirogyra crassa*, *Oedogonium* sp., Schenk (1858a), GERMANY; *Spirogyra* sp., Domján (*loc. cit.*), HUNGARY.

The sizes given in the Hungarian portion of Domján's paper are as follows: sporangia, $7.8-15.6 \mu$ wide by $7.8-15.6 \mu$ high; apophysis, $5.2-15.6 \mu$ wide by $5.2-11.25 \mu$ high; zoospores, 5.2μ in diameter. The last measurement is more than twice that given by Schenk (2μ). Since only the diameter of the sporangium is given by Schenk, Domján's figures on its height have not been included in the diagnosis.

From both Schenk's and Domján's accounts, the apophysis often equals and even exceeds the diameter of the sporangium. Schenk observed that zoospores were formed in the apophysis as well as in the sporangium.

The separation of the inoperculate form first observed by Schenk from the operculate which he found soon after has been suggested before (Sparrow, 1936a:437), and Domján's placing of the fungus in *Phlyctochytrium* appears wholly justifiable.

PHLYCTOCHYTRIUM LATERALE Sparrow

J. Linn. Soc. London (Bot.), 50:445, pl. 17, figs. 6-10. 1936

Sporangium sessile, subspherical or domelike, $10-13 \mu$ in height by $12-15 \mu$ in diameter, wall smooth, thin, colorless; rhizoids branched or occasionally unbranched, arising from a main axis which emerges somewhat laterally from a subspherical subsporangial apophysis $6-7 \mu$ high by $9-10 \mu$ in diameter; zoospores spherical, $4-5 \mu$ in diameter, with a prominent eccentric colorless globule and a single flagellum, liberated successively through a fairly large apical pore; resting

spore sessile, spherical, 12μ in diameter, with a smooth thick wall, contents with a large colorless centric globule, rhizoidal system stout, branching, arising from a subsporangial apophysis, germination not observed.

Parasitic on *Spirogyra sp.*, ENGLAND.

The formation of a single relatively stout rhizoidal axis which arises laterally from the apophysis segregates the species from *Phlyctochytrium Lagenaria*.

PHLYCTOCHYTRIUM CHAETOPHORAE de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:46. 1896

Rhizidium Chaetophorae de Wildeman, La Notarisia, 10 (3):35. 1895;

Ann. Soc. Belge Micro. (Mém.), 19:217, pl. 7, figs. 15-21. 1895.

Sporangium sessile or on a slender stalk, narrowly obpyriform, rarely ellipsoidal, $20-38 \mu$ long by $15-20 \mu$ in diameter, wall smooth, thin, colorless; endobiotic part consisting of an ovoid subsporangial swelling with a few scarcely visible rhizoids; zoospores about 3μ in diameter, emerging through a broad apical pore with an irregular margin; resting spore unknown.

On *Chaetophora elegans*, coll. Goffart, BELGIUM.

No information is given on the number of flagella on the zoospores.

PHLYCTOCHYTRIUM SYNCHYTRII Köhler

Arb. biol. Abt. (Anst.-Reichsanst.) Berlin, 13:382, pls. 1-2. 1924

Sporangium sessile, usually spherical, up to 50μ or more in diameter, with from one to nine strongly protruding finger-like papillae, wall smooth, slightly thickened, colorless; endobiotic part very thin-walled, irregularly expanded or subspherical, flattened against the host wall; zoospores spherical, 4μ in diameter (occasionally 4.5μ or more), with one or several minute eccentric oil droplets and a flagellum $20-25 \mu$ long, discharged through the nearly sessile circular pores 4μ in diameter formed upon the deliquescence of the papillae; resting spore epibiotic, spherical (?), 14μ in diameter, colorless, with a roughened outer wall, upon germination forming a spherical sporangium 9μ in diameter.

Parasitic on resting sporangia of *Synchytrium endobioticum*, GERMANY.

Profuse development of sporangia occurred when the host sporangia were spread out on moist gypsum blocks.

PHLYCTOCHYTRIUM BIPOROSUM Couch

J. Elisha Mitchell Sci. Soc., 47:254, pl. 17, figs. 52-65. 1932

Sporangium sessile, spherical or ovoid at first, becoming truncated and angular in outline upon the formation of two broad oppositely placed apical sessile or slightly elevated discharge papillae, 10-12 μ high by 8-13 μ in diameter, wall delicate, disappearing soon after zoospore discharge, smooth, colorless; rhizoid somewhat broad, unbranched or branched, slightly expanded immediately beneath the host wall; zoospores spherical or somewhat ovoid, 2-2.6 μ in diameter, with a minute refractive basal granule and a long flagellum, emerging through two pores formed upon the deliquescence or bursting of the two discharge papillae, movement amoeboid or swimming; resting spore not observed.

On *Vaucheria* sp., *Bumilleria* sp., *Oedogonium* sp., Couch (*loc. cit.*), *Spirogyra* sp., Sparrow (1933c:522, fig. I, 19-20), UNITED STATES; (?) *Spirogyra* sp., Sparrow (1936a:443, fig. 3 m-p), ENGLAND (see *Rhizophydiuum Haynaldii*, p. 179).

The very slight development of the subsporangial apophysis, which in some cases is completely lacking, makes the generic disposition of the species difficult. Couch could not be certain that the rhizoid branched, but such branches have been observed by Sparrow (1933c). The zoospores of Sparrow's fungus differed from Couch's in having a colorless centric globule. Sparrow has tentatively referred to this species a fungus found on *Spirogyra* in England which has sporangia essentially like those of Couch's fungus save that the papillae are more definitely elevated, the zoospores slightly larger (3 μ), and the unbranched (rarely branched) rhizoid never expanded to form a subsporangial apophysis. In these respects it approaches *Rhizophydiuum Haynaldii* and the incompletely known *R. rostellatum* (de Wildeman) Fischer.

Further study will be necessary to determine the degree of variability of the rhizoidal system in this fungus before it can be said with certainty that all these biporous forms belong to a single species.

PHLYCTOCHYTRIUM CHAETIFERUM Karling

Mycologia, 29:179, figs. 1-3. 1937

Sporangia sessile, broadly pyriform, ovoid, or subspherical, with a broad protruding apical papilla, 12-30 μ high by 18-45 μ in diameter, the subspherical ones 15-47 μ in diameter, wall somewhat thickened, colorless, covered by from three to thirty or more delicate flexible branching hairs up to or exceeding 200 μ in length; rhizoids one or several, branched, extensive, arising from one to several main axes which branch off from a spherical (8-11 μ in diameter), irregular, elongated, or fusiform subsporangial apophysis; zoospores spherical, 2.5-4 μ in diameter, with a highly refractive colorless centric globule and a long flagellum, emerging in a group surrounded by an evanescent vesicle or individually; resting spore ovoid or subspherical, from 9 μ (high?) \times 10 μ (in diameter?) to 14 \times 17 μ , or spherical and 10-17 μ in diameter, wall smooth, moderately thick, colorless, contents with one or more large oil globules, endobiotic system like that of the sporangium, germination not observed. (Modified from Karling.)

Saprophytic on cells of *Hydrodictyon reticulatum*, *Oedogonium* sp., Karling (*loc. cit.*), *Cladophora* sp., Sparrow (MICHIGAN), UNITED STATES.

PHLYCTOCHYTRIUM PLANICORNE Atkinson

Bot. Gaz., 48:337, fig. 7. 1909

(Figure 10I, p. 152)

Sporangium sessile, occasionally stalked, broadly ellipsoidal, narrowly to broadly ovoid, or narrowly pyriform, variable in size, 6-24 μ high by 6-17 μ in diameter, wall thin, colorless, smooth, bearing at the apex and around the discharge papilla a collarette of four (rarely six) solid highly refractive slightly converging plain teeth rarely more than 4 μ high; rhizoidal system extremely variable in its development, consisting of a few short branches or an extensive much-branched complex, in either type arising from a fusiform to spherical subsporangial apophysis 3-13 μ in diameter when spherical, when subspherical up to 12 μ in diameter by 10 μ high; zoospores spherical, 3-6 μ in diameter, with a prominent eccentric colorless globule about 3 μ in diameter and a few minute droplets in the plasma, flagellum about 30 μ long, emerging individually through an apical

pore and eventually swimming away or discharged in a compact group possibly surrounded by an evanescent vesicle, movement swimming or amoeboid; resting spore not observed.

Parasitic on *Spirogyra varians*, Atkinson (*loc. cit.*), *Rhizoclonium hieroglyphicum*, *Spirogyra* sp., Sparrow (1932b:279, fig. 3 e-k), saprophytic on *Cladophora* sp., *Oedogonium* sp., Sparrow (1938c:486, figs. 1-6), saprophytic in decaying stems of *Acorus Calamus*, Sparrow (MICHIGAN), UNITED STATES.

PHLYCTOCHYTRIUM ZYGNEMATIS (Rosen) Schroeter

Engler and Prantl, Natürlichen Pflanzenfam., 1(1):79. 1892

Chytridium Zygnematis Rosen, in Cohn, Beitr. Biol. Pflanzen, 4:266, pl. 13, figs. 1-14, pl. 14, figs. 15-27. 1887.

Rhizidium Zygnematis (Rosen) Dangeard, Le Botaniste, 1:64. 1889.

Sporangium sessile or occasionally stalked, spherical or broadly ovoid, about 15-17 μ in diameter, with an apical collarette of four somewhat elevated, upright, solid, shallowly bipartite teeth which surround the discharge papilla; rhizoids well developed, branched, arising from the base or the sides of a spherical (about 7 μ in diameter), broadly ellipsoidal, or somewhat irregularly saclike subsporangial apophysis, sometimes apparently absent; zoospores spherical or somewhat ovoid, 3-4 μ in diameter, with a conspicuous eccentric colorless globule and a long flagellum, emerging in a compact mass, probably surrounded by the inner layer of sporangium wall, through an apical pore, movement hopping; resting spore not observed.

On *Zygnema cruciatum*, *Z. stellinum*, Rosen (*loc. cit.*), FRANCE (STRASBOURG); Minden (1915:343), GERMANY.

The sporangium in this species tends to be more spherical and the teeth are more shallowly cleft than in *Phlyctochytrium quadricorne* or *P. dentatum*.

Rosen's rather complete investigation of his species established the fact that the apophysis is a secondarily formed structure which appears on the endobiotic system after the establishment of the rhizoids. Remarkable variations in the character and the position of the apophysis and rhizoids were also noted. Abnormal forms with more than one apophysis, others with the apophysis outside the substratum rather than inside it, and so on, were described and figured. Smaller "Frostsporangien" frozen in the ice but still viable

were found. The species only attacked filaments of *Zygnema* which were in a moribund or enfeebled condition, and it could not be transferred to other, associated, algae.

PHLYCTOCHYTRIUM DENTATUM (Rosen) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:46. 1896

Chytridium dentatum Rosen, in Cohn, Beitr. Biol. Pflanzen, 4:266, pl. 14, fig. 29. 1887.

Rhizidium dentatum (Rosen) Dangeard, Le Botaniste, 1:64. 1889.

Sporangium sessile or occasionally stalked, somewhat cylindrical or ovoid, with four apical bipartite prominent converging teeth, wall thin, smooth, colorless; rhizoids delicate, branched, arising from several places on a spherical or subspherical subsporangial apophysis; zoospores and resting spores not observed.

On *Spirogyra orthospira*, Rosen (*loc. cit.*), FRANCE (STRASBOURG); *Spirogyra* sp. (coll. Scherffel), Domján (1936:43, pl. 1, figs. 96-97), HUNGARY.

Rosen was unsuccessful in his attempts to inoculate *Zygnema* and *Oedogonium* with this fungus.

The species resembles *Phlyctochytrium urceolare* in the shape of its sporangium, but differs in having four teeth rather than six.

Minden (1915:344) uses the binomial *Phlyctochytrium dentatum* (Rosen) Schroeter, but the combination was not actually used by Schroeter when he established the genus. Fischer (1892:110) calls it *Rhizidium dentatum* (Rosen) Fischer. In a list of Hungarian fungi Moesz (1938:72) uses the binomial *Phlyctidium dentatum* (Rosen) Schroeter. Since no such combination was apparently ever made by Schroeter, it is presumed that *Phlyctidium* was used in error for *Phlyctochytrium*.

PHLYCTOCHYTRIUM QUADRICORNE (de Bary) Schroeter

Engler and Prantl, Natürlichen Pflanzenfam., 1(1):79. 1892

Chytridium quadricorne de Bary. See Rosen, in Cohn, Beitr. Biol. Pflanzen, 4:266, pl. 14, fig. 28. 1887.

Rhizidium quadricorne (de Bary) Dangeard, Le Botaniste, 1:64. 1889.

Sporangium sessile, broadly cylindrical or broadly ovate, 10-11 μ high by 13 μ in diameter, with a rounded or flattened base, bearing an apical collarette of four solid upright deeply incised bipartite prominent teeth, wall fairly stout, colorless; rhizoids present or

absent, when present branched, arising from the base of a spherical (about 7μ in diameter) or occasionally fusiform subsporangial apophysis; zoospores spherical, 6μ in diameter, with an eccentric colorless globule and a long flagellum, emerging in a compact mass probably surrounded by a slime sheath through an apical pore formed within the collarette of teeth and resting motionless for a time before assuming individual motility, movement hopping or amoeboid; resting spore not observed.

On *Oedogonium rivulare*, de Bary (in Rosen, 1887), FRANCE (STRASBOURG); *Vaucheria polysperma*, Scherffel (1926a:224, pl. 10, figs. 105-106), HUNGARY; substratum (?), Karling (1932:49, fig. 19), *Cladophora* sp., Sparrow (1933c:523, text fig. I, 4, resting spore?), UNITED STATES; *Cladophora* sp., Sparrow (1936a:445, fig. 4o), ENGLAND.

A glycerin mount of the type material is in the British Museum (N. H.), in the de Bary collection, but it was not available for examination in 1940.

Scherffel (*loc. cit.*) has used the binomial *Rhizidium quadricorne* de Bary; there appears to be no evidence, however, that de Bary ever cited his fungus in this manner.

A thick-walled subspherical resting body 15μ in diameter has been found in certain sporangia of this species (Sparrow, 1933c). It may belong to an extraneous parasitic organism.

The teeth of the fungus figured by Karling (*loc. cit.*) are more like those of *Phlyctochytrium Zyg nematis* (Rosen, *op. cit.*, pl. 13, fig. 12, lower), being shallowly rather than deeply incised. Too little is known at present of these species to judge how much weight is to be given variations of this nature.

A form with nearly spherical sporangia and four strongly diverging bipartite teeth found by Sparrow (1938c:fig. 33) on *Cladophora* in Michigan is perhaps referable to this species.

PHLYCTOCHYTRIUM BULLATUM Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:296. 1937; Amer. J. Bot., 25:487,
figs. 7-14. 1938
(Figure 10H, p. 152)

Sporangium subspherical or broadly urn-shaped, $10.5-23 \mu$ high by $12-26 \mu$ in diameter, colorless, with two concentric whorls of solid

apical converging teeth, the inner circle being composed of four minute divergently bipartite sessile ones which immediately surround the discharge papilla, the outer circle, of six bipartite strongly diverging longer ones each of which terminates the inwardly arching tip of a broad flangelike solid boss 5–7 μ long by 3 μ wide by 3–5 μ high; endobiotic system composed of a broadly fusiform sometimes spherical or irregular subsporangial swelling, 10–20 μ wide by 6–10 μ high, from one side or, occasionally, from opposite sides of which emerges a wide rhizoid which usually branches at some distance from the swelling and ramifies through one or more cells of the alga; zoospores spherical, 8 μ in diameter, the clear plasma containing a single large slightly eccentric spherical or hemispherical oil globule, 4–5 μ in diameter, and a few minute peripheral granules, with a single posterior flagellum about 40 μ in length; resting spores not observed.

Saprophytic and weakly parasitic on *Cladophora* sp., Sparrow (1933c: fig. I, 16), oögonia of *Vaucheria*, Sparrow (MICHIGAN), UNITED STATES.

PHLYCTOCHYTRIUM URCEOLARE Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:296. 1937; Amer. J. Bot., 25:491, figs. 31–41. 1938

Sporangium colorless, somewhat variable in shape but predominantly cylindrical and expanding slightly distally until reaching the first whorl, which is composed of six sessile bipartite solid upright or slightly diverging teeth, where it tapers sharply toward the apical discharge papilla, which is surrounded by a whorl of four minute bipartite upright solid teeth, 10–14 μ high by 7–11 μ in diameter tapering to 5–6 μ at the apex; endobiotic system composed of a narrowly to broadly fusiform or occasionally spherical subsporangial swelling 3–5 μ in diameter by 7–10 μ in height (3–7 μ in spherical examples), the swelling if narrowly fusiform generally bearing at its base a single rhizoid which ultimately branches, if broadly fusiform or spherical, bearing two oppositely placed rhizoids which eventually branch; zoospores spherical, 4 μ in diameter, with a single slightly eccentric spherical colorless oil globule 2 μ in diameter and a single posterior flagellum about 20 μ in length; resting spores not observed.

Saprophytic and weakly parasitic on *Cladophora* sp., UNITED STATES.

Probably identical with the fungus incompletely observed on *Cladophora* from Ithaca, New York (Sparrow, 1933c:523, text fig. I, 3). It differs from *Phlyctochytrium dentiferum* in having a more cylindrical sporangium, which is slightly expanded distally up to the place of emergence of the outer whorl of teeth, where it tapers sharply toward the blunt rounded papillate apex. The papilla is surrounded by the inner whorl of teeth.

PHLYCTOCHYTRIUM DENTIFERUM Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:295. 1937; Amer. J. Bot., 25:489, figs. 15-32. 1938

Sporangium slightly subspherical, 10-15 μ high by 10-14 μ in diameter, colorless, with two apical concentric whorls of solid converging apical teeth, the inner circle being composed of four minute (about 2 μ high by 2 μ wide) divergently bipartite sessile ones which immediately surround the discharge papilla, the outer, of six larger (about 4 μ high by 2.5 μ wide) bipartite sessile or slightly elevated ones; endobiotic system composed of a broadly fusiform spherical or irregular subsporangial swelling, 5-15 μ in diameter by 5-12 μ in height, from opposite sides of which emerges a moderately broad distally branching rhizoid; zoospores spherical, 7 μ in diameter, with a single large slightly eccentric colorless oil globule 4 μ in diameter and a single posterior flagellum about 30 μ in length; resting spore not observed.

Saprophytic and weakly parasitic on *Cladophora* sp., UNITED STATES.

IMPERFECTLY KNOWN SPECIES OF PHLYCTOCHYTRIUM

? **PHLYCTOCHYTRIUM AUTRANI de Wildeman**

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:46. 1896

Rhizidium (?) *Autrani* de Wildeman, Ann. Soc. Belge Micro. (Mém.), 19:72, pl. 2, figs. 17-21. 1895.

Epibiotic body consisting of a terminal globular structure with a slightly elevated apical pore and a basal ovoid-elongate generally clavate part, the two united by a short or somewhat elongate constricted isthmus; rhizoid consisting of an endobiotic needle-like stalk; zoospores and resting spore not observed.

On *Cosmarium*, SWITZERLAND.

The species may ultimately be referred to *Scherffeliomyces*.

? *PHLYCTOCHYTRIUM CATENATUM* (Dang.) Schroeter

Engler and Prantl., Natürlichen Pflanzenfam., 1(1):79. 1892

Rhizidium catenatum Dangeard, Le Botaniste, 1:65, pl. 3, fig. 24 a-b.
1889.

Sporangium obpyriform, with three or four lateral or basal swellings on its outer surface, wall colorless, relatively thick; rhizoids branched, arising from a subsporangial apophysis; zoospores spherical, 3μ in diameter, with a colorless globule, escaping through a sessile or slightly elevated apical pore; resting spore not observed.

In cells of *Nitella tenuissima*, FRANCE.

Fischer and Minden think that this species forms epibiotic sessile sporangia. Dangeard does not describe their position in relation to the host cell. From the fact that comparison is made in the description with *Diplophlyctis intestina* it is very probable that the fungus is entirely endobiotic and hence not a species of *Phlyctochytrium*, but rather of *Diplophlyctis*.

Fischer and Minden also believe the swellings on the surface of the sporangium to be quiescent zoospores. Scherffel (1925b:48), however, suggests that they may be male cells similar to those found in some species of *Rhizophydiump*.

? *PHLYCTOCHYTRIUM DESMIDIACEARUM* Dangeard

Le Botaniste, 28:196, pl. 19, figs. 1, 3-9, 11-20. 1937

Sporangium sessile, narrowly to broadly ovoid or somewhat narrowly urceolate, with an apical collarette of not more than four bipartite shallowly cleft prominent teeth, wall thin, smooth, colorless; rhizoids branched, arising from a main axis at the base of a broadly fusiform or spherical subsporangial apophysis; zoospores spherical, $2-3 \mu$ in diameter, with a colorless eccentric globule and a long flagellum, escaping through a large apical pore; resting spore asexually formed, extramatrical, generally sessile, spherical, $20-25 \mu$ in diameter, with a thickened smooth colorless wall, contents with a large central vacuole surrounded by numerous small globules, endo-

biotic system like that of the sporangium but usually with a much smaller apophysis, germination not observed.

On *Closterium Ehrenbergii* and related species and on *Netrium digitus*, FRANCE.

Since observations on the precise number and arrangement of the teeth were incomplete the species cannot be adequately defined. It is of interest, however, because of the resting spores, this being probably the first undoubted instance of their occurrence in the *Dentigera* group (see *Phlyctochytrium quadricorne*, p. 231).

Observations of great biological interest were made by Dangeard on the reaction of the host to the parasite (see p. 72).

A sequence of development similar to that found in *Chytridium Lagenaria* was observed in this species. After infection the endobiotic system reached nearly its full size and complexity before growth of the epibiotic part—the case of the infecting zoospore—was initiated.

? *PHLYCTOCHYTRIUM PANDORINAE* (Wille) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:47. 1896

Chytridium (Phlyctidium) Pandorinae Wille, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 8, Afd. 1, No. 18:46, pl. 2, fig. 86. 1884.

Rhizidium Pandorinae (Wille) Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4):109. 1892.

Sporangium partly imbedded in the gelatinous sheath of the host colony, subspherical, with an apical wartlike protuberance and an apical or subapical elevated discharge pore; subsporangial part tubular, inflated in the mid-region, terminating on the surface of the host cell wall; zoospores and resting spore not observed.

On *Pandorina morum*, URUGUAY.

? *PHLYCTOCHYTRIUM SPIROGYRAE* de Wildeman

Ann. Soc. Belge Micro. (Mém.), 20:48. 1896

Rhizidiomyces Spirogyrae de Wildeman, Ann. Soc. Belge Micro. (Mém.), 19:111, pl. 4, figs. 14-22. 1895.

Sporangium sessile, spherical or slightly ovoid, wall thin, smooth, colorless; rhizoids of limited extent, branching within the zygospore of the host, arising from a fairly large spherical or ovoidal endobiotic

subsporangial apophysis which rests either on the wall of the zygosore or in the contents; zoospores not observed, presumably escaping through a broad apical slightly protruding pore, the sporangium proliferating; resting spore endobiotic, lodged either in the zygosore or the gametangium, spherical or ovoid, with a thickened (rough?) wall, germination not observed.

On zygospores of *Spirogyra*, FRANCE.

From the position of the resting spores, it is possible that this is a species of *Chytridium* with proliferating sporangia. Observations on the discharge of the zoospores are necessary before it can be placed generically and the apparent proliferation confirmed.

EXCLUDED SPECIES OF *PHLYCTOCHYTRIUM*

* *PHLYCTOCHYTRIUM EUGLENAE* (Dang.) Schroeter

Engler and Prantl, *Natürlichen Pflanzenfam.*, 1(1):79. 1892

Rhizidium Euglenae Dangeard, *Ann. Sci. Nat. Bot.*, VII, 4:301, pl. 13, figs. 11-19. 1886; *Le Botaniste*, 1:64, pl. 3, fig. 22. 1889.

Sporangium narrowly elongate-pyriform, ovoid, subspherical, or somewhat angular and irregular, 30μ long by $10-18 \mu$ in diameter, wall thin, smooth, borne on a spherical apophysis about $5-6 \mu$ in diameter, which either rests directly on the wall of the host cell or is attached to it by a slender unbranched stalk; endobiotic rhizoid an unbranched tube; zoospores spherical, 2μ in diameter, with a basal colorless globule and a flagellum, discharged through a single apical pore (rarely two); resting spore spherical, thick-walled, brownish, the outer surface either smooth, slightly verrucose, or covered with short slender spines, borne on an extramatrical or endobiotic spherical apophysis from the base of which a slender unbranched filament arises, germination not observed.

Parasitic on resting cells of *Euglena*, Dangeard (*loc. cit.*), FRANCE; (coll. Marchal) de Wildeman (1890:11, fig. 2), BELGIUM.

Since the apophysis of the sporangium is epibiotic the species cannot be placed in *Phlyctochytrium* as here defined. The resting spores first described for this species (Dangeard, 1886a) differ from those described in the 1889 paper in being rough-walled and not apophysate, rather than spiny-walled and apophysate. There is a strong possibility that two different organisms are involved.

Dangeard pointed out that the position of the apophysis (whether sessile or borne on a stalk) depended upon the proximity of the germinating zoospore to the host cell. Thus, if the zoospore was at some distance from the *Euglena* a stalk was formed, otherwise the apophysis was sessile. He distinguished two forms of his fungus: (1) "Chytridium-Form" in which the apophysis was endobiotic, and (2) "Rhizidium-Form" in which it was epibiotic. It is possible the "Chytridium-Form" is in reality another fungus. As understood here, the species forms typically an epibiotic apophysis.

Minden identifies with Dangeard's organism a fungus discussed by Schenk (1858a:246) as *Chytridium Euglenae* Braun, and uses the binomial *Phlyctochytrium Euglenae* (Schenk) Schroeter. Schenk, however, was unquestionably dealing with *Polyphagus Euglenae*. Furthermore, Schenk's fungus, though described in the course of a discussion of Braun's genus *Rhizidium*, was always referred to by him as *Chytridium Euglenae* and not *Rhizidium Euglenae*, as Minden implies. It is interesting to note that Minden (1915:383) in describing *Polyphagus Euglenae* asserts that Schenk's fungus belongs in *Polyphagus*. See also *Chytridium Euglenae* Braun, page 355.

Dangeard's fungus is considered by Minden to be synonymous with *Saccommycetes Dangeardii* (S. *endogenus*).

Braun's *Chytridium Euglenae*, collected by von Siebold and Meissner, is probably identical with the present species. It is too little known to be considered here, however.

* *PHLYCTOCHYTRIUM STELLATUM* H. E. Petersen

Bot. Tidsskrift, 29:417. 1909; Ann. Mycologici, 8:550, fig. xxiii. 1910

Sporangium ovoid or somewhat irregular, $11-12 \times 15-16 \mu$ (small forms 8μ in diameter), wall colorless, thin, collapsing when empty, sporangium arising as a lateral outgrowth from the endobiotic swelling or at the boundary of the epi- and endobiotic parts, the case of the zoospore persistent; endobiotic part consisting of a spherical ($6-8 \mu$ in diameter) or fusiform swelling beneath the zoospore case, producing basally a rhizoid from which lateral branches arise; zoospores spherical, with a colorless globule and a posterior flagellum, movement hopping; resting spore asexually formed directly from the contents of the endobiotic swelling, spherical, $15-18 \mu$ in diameter, colorless, contents with a large oil globule, the outer wall covered

by short thick spines which later may become prominent solid clavate rods 3–6 μ long by 4 μ thick at the tips, germination not observed.

In *Spirogyra*, Petersen (*loc. cit.*), DENMARK; *Zygnema*, Scherffel (1926a:233, pl. 10, figs. 118–124), HUNGARY.

Scherffel has given the most complete account of this species. From the development as described by him and from the position of the resting spore, the fungus is clearly no *Phlyctochytrium*. Neither Scherffel nor Petersen makes clear whether the sporangium is endo- or epibiotic. From Scherffel's figures it may be either. The relationships of the parts are lost or confused, probably because of mounting on a slide. Scherffel apparently believes the species to be intermediate between *Entophyscitis* and *Phlyctochytrium*. Minden considers it near *E. bulligera*. Possibly it is a form occurring on a thin-walled host with a method of development similar to that of *Chytridium Schenkii*.

BLYTTIOMYCES BARTSCH

Mycologia, 31:559. 1939

(Figure 12A, p. 244)

"Thalli partly intra- and extramatrical, monocentric, eucarpic. Zoosporangia extramatrical, globose, inoperculate, provided with an apiculus developing from distal portion of zoospore case, with sub-apical exit pore; forming by enlargement of extramatrical spore and delimited from intramatrical portion of thallus by a septum. Zoospores uniguttulate, uniflagellate. Intramatrical portion of thallus coarse, extensive, consisting of 2, rarely 3, apophyses, the distal one bearing a branched rhizoidal system. Resting spores intramatrical, variable in shape, forming by growth and encystment of an apophysis; germinating by the formation of an extramatrical sporangium liberating zoospores" (Bartsch, *loc. cit.*).

In zygospores of *Spirogyra*.

A monotypic genus, possibly related to *Chytridium*. Bartsch has aptly pointed out that the apiculus though suggesting a non-functional operculum has a different origin. In *Blyttiomycetes* it is laid down very early in the formation of the thallus and remains throughout development as a distinct structure. In operculate

chytrids, on the other hand, the operculum forms relatively late, as a modification of the apex of the discharge papilla.

BLYTTIOMYCES SPINULOSUS (Blytt) Bartsch

Mycologia, 31:559, figs. 1-24. 1939

Chytridium spinulosum Blytt, Vidensk. Selsk. Skr. Christiana (Mat.-Nat. Kl.), 1882(5):27.

"Zoosporangia multisored, aggregated, globose, inoperculate, hyaline, aculeated, $14.2-28 \times 16.8-32.3$, averaging 23.4μ in diameter $\times 28.2 \mu$ high exclusive of apiculus; with a single lateral exit pore about 40° from apex; aculei narrow, hyaline, about $0.5-2.0 \mu$ long, with rounded apices; apiculus cuculate, hyaline, smooth-walled, 5.6μ in diameter $\times 3.5-4.9$, averaging 3.8μ high. Zoospores spherical to ovoid, hyaline, $4.2-7.0 \mu$ in diameter, with a large, clear, refractive globule; flagellum approximately 25μ long; zoospore case becoming thickened distally, persisting as sporangial apiculus after germination. Intramatrical portion of thallus coarse, extensive; consisting of 2 tandem apophyses separated by zygospore wall of host, rarely with 3 apophyses, and with an extensive, branched rhizoid, up to 3.6μ in diameter, extending from distal apophysis, tapering to delicate points. Apophyses spherical, ovoid or spindle-shaped, with smooth, hyaline membrane; proximal apophysis $5.6-7.0$, averaging 5.9μ in diameter, distal one $4.2-21.1$, averaging 11.2μ in diameter. Resting spores smooth, spherical, ovoid or irregular, $14.0-32.2$, averaging 22.2μ in diameter, with 2-layered, hyaline wall $3.0-5.0 \mu$ thick; endospore $2.0-3.8 \mu$, exospore about $1.0-1.2 \mu$ thick; with finely granular cytoplasm, containing 1 to several oleaginous-like globules; germinating by the formation of an extramatrical, aculeated sporangium lacking an apiculus; liberating zoospores" (Bartsch, loc. cit.).

Parasitic and saprophytic in zygospores of *Spirogyra majuscula*, S. Weberi, Bartsch (loc. cit.), UNITED STATES; *Spirogyra sp.*, Blytt (loc. cit.), NORWAY; *Spirogyra sp.*, H. E. Petersen (1909:409, fig. xix; 1910:543, fig. xix), DENMARK; *Spirogyra sp.*, Scherffel (1926a:216, pl. 10, figs. 90-95), HUNGARY; *Spirogyra majuscula*, Denis (1926:19, fig. 3), FRANCE; *Spirogyra sp.*, Cejp (1932a:1, pl. 1, figs. 1-4, pl. 2, figs. 1-2), GERMANY.

RHIZIDIOPSIS SPARROW

Trans. Brit. Mycol. Soc., 18:216. 1933; J. Linn. Soc. London (Bot.), 50:450.
1936

(Figure 12 B-E, p. 244)

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming the rudiment of the sporangium, which consists of the body of the encysted zoospore and, continuous with it, the greatly expanded extramatrical germ tube, the endobiotic part rhizoidal; sporangium inoperculate, epibiotic, formed from the sporangial rudiment; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium; rhizoidal system endobiotic, branched, arising from the tip of the penetration tube; resting spore small, epibiotic, thick-walled, apparently asexually produced, upon germination forming a zoosporangium at its apex and concomitant with its body.

On diatoms.

The developmental features of *Rhizidiopsis* present another variation of the *Chytridium* type and resemble closely those of *Chytridium Schenkii* and *Podochytrium*. In contrast to the latter genus, however, no sterile base is ever formed, and both the cyst and its outgrowth are fertile. The resting spore is small and has evidently been produced from a single zoospore which has encysted on the surface of the alga, possibly developed a rhizoidal system (although this was not observed), and, without enlargement of its body, been transformed into a thick-walled resting spore.

RHIZIDIOPSIS EMMANUELENSIS Sparrow

Trans. Brit. Mycol. Soc., 18:216. 1933; J. Linn. Soc. London (Bot.), 50:
451, pl. 18, figs. 1-13. 1936

Sporangium smooth-walled, pyriform or clavate, 6-12 μ long by 5-10 μ in diameter, the long axis generally parallel with that of the algal filament, attached by its narrower end to, and continuous with, the rounded cyst of the zoospore, which is 3-4 μ in diameter, forming from four to twelve or more zoospores 3-4 μ in diameter which at maturity are discharged through a single apical pore; resting spore spherical or somewhat flattened, thick-walled, 4-4.5 μ in diameter,

surrounded by a dark-brown rough incrustation, upon germination producing a sporangium.

Parasitic on *Melosira varians* and *Nitzschia* (?) sp., ENGLAND.

PHYSORHIZOPHIDIUM SCHERFFEL

Arch. Protistenk., 54:181. 1926

(Figure 10G, p. 152)

Thallus epi- and endobiotic, monocentric; sporangium inoperculate, formed near the surface of the substratum from the enlarged body of the encysted zoospore and producing by the deliquescence of a papilla one or more pores for the escape of the zoospores; thallus with an endobiotic swelling with or without rhizoids and a secondarily formed epibiotic subsporangial swelling; zoospores posteriorly uniflagellate, produced within the sporangium, with a single oil droplet; resting spore not observed.

On diatoms.

Distinct from *Phlyctidium* and *Rhizophydis* primarily in the secondary formation of a subsporangial epibiotic knoblike swelling.

PHYSORHIZOPHIDIUM PACHYDERMUM Scherffel

Arch. Protistenk., 54:181, pl. 9, figs. 21-40. 1926

Sporangium at first spherical, by the formation of a broad conical truncate outgrowth from one side becoming at maturity ovate, humped, or irregular, $8-21.6 \mu$ high by $10-27 \mu$ long, generally with the long axis at right angles to that of the penetration tube, with a thick smooth wall on which is formed at or near the tip of the conical lateral outgrowth a single prominent conical basally, laterally, or apically directed thin-walled discharge papilla; haustorium typically spherical, provided with delicate branched rhizoids (?) and, between the outer surface of host wall and the base of sporangium, with an epibiotic, subsporangial swelling of the same size as or slightly larger than the haustorium; zoospores spherical, 2.7μ in diameter, with a single minute (less than 1μ) eccentric basal oil droplet and a posterior flagellum from four to five times as long as the body, emerging actively through a pore $3-7 \mu$ in diameter formed upon the deliquescence of the papilla; resting spore not observed.

Parasitic on *Amphora ovalis*, Scherffel (*loc. cit.*), HUNGARY; *Navicula sp.*, Sparrow, UNITED STATES (MICHIGAN).

Scherffel observed that the parasites avoided the girdle-band face and bored through the siliceous cell wall.

PODOCHYTRIUM Pfitzer

Sitzungsber. Niederrhein. Gesell. Natur- und Heilkunde, 1869:62. 1870

(Figure 12 K-L, p. 244)

Septocarpus Zopf, Nova Acta Acad. Leop.-Carol., 52:348. 1888.

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part consisting of the unexpanded body of the encysted zoospore and an apical prolongation, the endobiotic part rhizoidal, arising from the tip of a needle-like penetration tube; sporangium inoperculate, epibiotic, formed from the apical prolongation of the sterile epibiotic cyst of the zoospore, from which it is separated by a cross wall; zoospores posteriorly uniflagellate, with a single globule; resting spore not observed.

The two species, so far as is now known, are confined to diatoms.

KEY TO THE SPECIES OF PODOCHYTRIUM

- Sporangium clavate..... *P. clavatum*, p. 243
Sporangium lanceolate..... *P. lanceolatum*, p. 245

PODOCHYTRIUM CLAVATUM Pfitzer

Sitzungsber. Niederrhein. Gesell. Natur- und Heilkunde, 1869:62. 1870

(Figure 12 L, p. 244)

Septocarpus corynephorus Zopf, Nova Acta Acad. Leop.-Carol., 52:348, pl. 20, figs. 21-28. 1888.

Sporangium sessile, occasionally borne on a short needle-like portion of the penetration tube, clavate or obpyriform, wall smooth, often stout, colorless, not giving a cellulose reaction, 8-19.2 μ high by 5-8.4 μ in diameter, resting directly on a knoblike sterile basal cell, 2.5-3 μ in diameter; rhizoids extremely delicate, branched, arising from the tip of a sometimes prolonged penetration tube; zoospores spherical, 3 μ in diameter, with a single colorless slightly eccentric

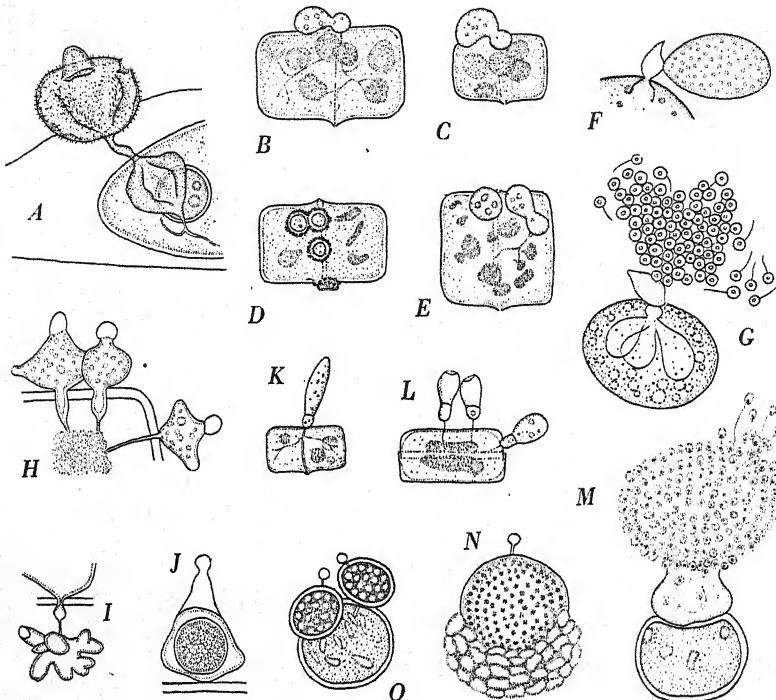


FIG. 12. Phlyctidiaceae

A. Blyttiomycetes spinulosus (Blytt) Bartsch, empty sporangium on zygospore of *Spirogyra*; spiny sporangium is epibiotic on surface of host gametangium; apiculus is terminal, discharge pore lateral; apophysis is within zygospore of host and gives rise at its base to rhizoidal system; resting spore is endobiotic. *B-E. Rhizidiopsis emmanuelensis* Sparrow ($\times 650$) on *Melosira*: *B-C*, *E*, maturing sporangia on surface of host; main body is produced as outgrowth from cyst of infecting zoospore; *D*, epibiotic resting spores. *F-G. Saccomyces endogenus* (Nowak.) Sparrow on *Euglena*: *F*, prosporangium on outer surface of encysted host; sporangium appears as broad lateral outgrowth; *G*, release of zoospores upon bursting of sporangium wall; endobiotic apophysis and broad finger-like lobes of haustorial system are apparent within the *Euglena*. *H-J. Coralliochytrium Scherffelii* Domján ($\times 650$) on *Zygnema*: *H*, group of sporangia with adherent cysts on surface of host cell; *I*, base of sporangium with endobiotic apophysis and stalk at tip of which is knarled digitate absorbing organ; *J*, epibiotic resting spore on surface of host. *K. Podochytrium lanceolatum* Sparrow ($\times 400$) on cell of *Melosira*. *L. Podochytrium clavatum* Pfitzer ($\times 650$) on cell of *Fragellaria*. *M-O. Scherf-*

globule, sometimes moving within the sporangium, emerging upon the dissolution of a broad scarcely visible apical papilla and either forming a temporary motionless mass at the orifice or swimming directly away; resting spore not observed (?).

Parasitic on *Pinnularia*, Pfitzer (*loc. cit.*), Zopf (*loc. cit.*), GERMANY; various diatoms, de Wildeman (1890:26), BELGIUM; *Melosira*, de Wildeman (1894:157), FRANCE; *Pinnularia*, *Melosira varians*, *Amphora*, *Gomphonema micropus* (possibly resting spore of fungus), Scherffel (1926a:174, pl. 9, figs. 13-16), HUNGARY; *Navicula spp.*, Sparrow (1933c:524, text fig. I, 13), UNITED STATES; *Fragellaria sp.*, Sparrow (1936a:449, fig. 4 b, g-h), ENGLAND; *Tabellaria flacculosa*, Tokunaga (1934b:391, pl. 11, figs. 11-12), JAPAN.

Scherffel has described an epibiotic "stopper-like" resting spore, 6-8 μ long by 4-5 μ thick, with rounded apex, smooth thickened wall, and fatty contents as possibly belonging to this species. The resting structure was borne in the larger, upper, part of a septate toplike body, the lower part of which was empty.

Whereas Zopf observed the fungus to gain entrance into the host only at the unsilicified line of fusion of the valves, Scherffel has noted that germinating zoospores may in some cases bore through the valve at any point.

PODOCHYTRIUM LANCEOLATUM Sparrow

Trans. Brit. Mycol. Soc., 18:216. 1933; J. Linn. Soc. London (Bot.), 50:450,
fig. 4c-f. 1936

(Figure 12 K)

Sporangium sessile, lanceolate or somewhat fusiform, often slightly tilted, with a small apical papilla, wall smooth, colorless, 20-25 μ high by 8-10 μ in diameter, tapering at each end to 3-4 μ , resting upon a sterile cuplike or occasionally knoblike base 4-5 μ in diameter; rhizoidal system consisting of a few sparsely branched rhizoids arising from the tip of a prolonged needle-like penetration tube;

felomyces parasitans Sparrow ($\times 650$) on *Euglena*: *M*, discharging sporangium resting on host cell; *N*, mature sporangium with attached zoospore cyst; *O*, two epibiotic resting spores with attached zoospore cysts.

(*A*, Bartsch, 1939; *B-E*, *K-O*, Sparrow, 1936a; *F-G*, Serbinow, 1907; *H-J*, Domján, 1936)

zoospores spherical, 3-4 μ in diameter, with a single refractive eccentric globule and a long flagellum, emerging through a small apical pore formed upon the deliquescence of a papilla; resting spore not observed.

On *Melosira varians*, ENGLAND.

Differing from *Podochytrium clavatum* in the shape and greater length of its sporangium, smaller apical pore, and complete lack of a stalk on the sterile part. The species resembles to a certain degree the immature plant of *P. clavatum* figured by Zopf (1888: pl. 20, fig. 25e).

SACCOMYCES SERBINOW

Scripta Bot. Horti Univ. Imper. Petro., 24:162. 1907

(Figure 12 F-G, p. 244)

Thallus epi- and endobiotic, monocentric, eucarpic, consisting of the epibiotic rudiment of the prosporangium formed from the body of the encysted zoospore and the endobiotic vegetative system, which is often apophysate and broadly lobed, digitate, or saccate; prosporangium epibiotic, sessile; sporangium inoperculate, subapical or lateral, very thin-walled, ellipsoidal or long-tubular, bursting apart at maturity; zoospores posteriorly uniflagellate, with a single globule; resting spore asexually formed, borne like the sporangium, germination not observed.

On Euglenophyceae.

In its method of zoospore formation *Saccomyces* bears a resemblance to *Polyphagus*. The character and development of the endobiotic vegetative system, however, and the monophagous habit distinguish it from that genus.

SACCOMYCES ENDOGENUS (Nowak.), comb. nov.

Polyphagus endogenus Nowakowski, Akad. umiej. Krakowie.

Wydziat mat.-przyród., Pamietnik, 4:191, pl. 10, figs. 108-114. 1878.

Saccomyces Dangeardii Serbinow, Scripta Bot. Horti Univ. Imper. Petro., 24:162, pl. 6, figs. 22-33. 1907.

Prosporangium pyriform, about 5 μ high by 3 μ in diameter (calculated), with a pronounced apiculus, wall thin, smooth, colorless; sporangium broadly ellipsoidal or elongate-tubular, occasionally

branched, 15–30 μ long by 8–10 μ in diameter, wall delicate, evanescent; endobiotic part consisting of a subsporangial apophysis (occasionally absent), from the base of which protrude from two to four very broad distally swollen digitations; zoospores nearly spherical, 2 μ in diameter, with a colorless centric or eccentric globule and a long flagellum, escaping upon the bursting of the sporangium wall; resting spore spherical, about 10 μ in diameter, with a thick wall, the outer surface covered by coarse conical spines, germination not observed.

On encysted *Euglena* sp., Nowakowski (*loc. cit.*), GERMANY (?); *Euglena viridis* Serbinow (*loc. cit.*), RUSSIA.

There is little question but that this organism was first described and figured by Nowakowski. He did not always appear to recognize that the sporangium arose as a lateral outgrowth of a prosporangium, nor did he observe the often apophysate and strongly digitate character of the endobiotic part. His Figures 110–112 of the sporangial stage and Figure 114 of the resting stage are, however, strikingly similar to those of Serbinow and leave little doubt as to the identity of the organisms.

SCHERFFELIOMYCES SPARROW

Mycologia, 26:377. 1934; *J. Linn. Soc. London (Bot.)*, 50:446. 1936
(Figure 12 M-O, p. 244)

Scherffelia Sparrow, *Trans. Brit. Mycol. Soc.*, 18:216. 1933. Non
Scherffelia Pascher, *Hedwigia*, 52:281. 1912.

Thallus extramatrical, epibiotic, and endobiotic, monocentric, eucarpic, consisting of the extramatrical persistent cyst of the zoospore, the proximal part of the germ tube, the epibiotic expanded rudiment of the sporangium, and the endobiotic vegetative system; sporangium inoperculate, zoospores uniflagellate, with a single globule; resting spore thick-walled, borne like the sporangium, contents with globules, germination not observed.

Known only as parasites of *Chlamydomonas* and *Euglena*.

The genus appears closely allied to *Phlyctidium* and *Rhizophydiuum*, but differs in its peculiar method of development, first noted by Zopf (1884). *Coralliochytrium* has the same type of development, but,

unlike *Scherffeliomyces*, forms angular multiporous sporangia, a thick-walled apophysis, and a stubby branched haustorial system.

KEY TO THE SPECIES OF SCHERFFELIOMYCES

- Sporangium spherical or subspherical; globule of zoospore orange
S. parasitans, p. 248
- Sporangium pyriform; globule of zoospore colorless
S. appendiculatus, p. 248

SCHERFFELIOMYCES PARASITANS Sparrow

Mycologia, 26:377. 1934; J. Linn. Soc. London (Bot.), 50:446, pl. 18, figs. 14-28. 1936

(Figure 12 M-O, p. 244)

Scherffelia parasitans Sparrow, Trans. Brit. Mycol. Soc., 18:216. 1933.

Sporangium sessile, at first lachrymose, becoming spherical or subspherical at maturity, resting in the concavity formed by the collapsed host cell, 17-22 μ in diameter, joined by a narrow tube of varying length to the spherical (2.5-3 μ in diameter) cyst of the zoospore, contents at first colorless, at maturity charged with orange oil droplets, with a barely perceptible single short unbranched endobiotic tube; zoospores minute, innumerable, spherical or ovoid, 2-3 μ in diameter, with a single orange globule, emerging in a compact mass from the broad mouth of the sporangium and remaining for a few seconds at the orifice, the mass then becoming disorganized as the spores assume motility, movement swimming or strongly amoeboid; resting spore spherical or ovoid, thick-walled, brownish, 8-10 μ high by 10-14 μ in diameter, attached by a narrow, often somewhat curved tube to the spherical (3 μ in diameter) cystospore, germination not observed.

Parasitic on resting cells of *Euglena* sp., ENGLAND.

SCHERFFELIOMYCES APPENDICULATUS (Zopf) Sparrow

J. Linn. Soc. London (Bot.), 50:449. 1936

Rhizidium appendiculatum Zopf, Nova Acta Acad. Leop.-Carol., 47: 203, pl. 20, figs. 17-27. 1884.

Rhizophydiump appendiculatum (Zopf) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):101. 1892.

Sporangium within the gelatinous sheath of the host, sessile on the contents of the alga, pyriform, up to 14μ long by 11μ in diameter, with a prominent sometimes elongate apiculus, wall thin, smooth, colorless, cystospore ellipsoidal or ovoid, laterally attached by a short tube to the apiculus, contents colorless; rhizoidal system sparingly branched, arising from the tip of a short axis; zoospores from a few to twenty or thirty, spherical, with a basal colorless globule and a long flagellum, escaping through an apical pore; resting spore borne like the sporangium and similar to it in shape, wall thick, smooth, colorless, contents with one or with many globules.

Parasitic in the *Palmella* stage of *Chlamydomonas* sp. and in immature swarmers within the mother cell, never on moving individuals, Zopf (*loc. cit.*), GERMANY; Scherffel (1914), HUNGARY.

The organism occurred in epidemic proportions in Zopf's material. De Wildeman (1895a:71) has referred to this species a fungus on an undetermined alga from Switzerland. No appendicular structure was observed, however, and he rightly suggests the possibility that it may be *Rhizophyllum simplex*. Similarly, Cook (1932a:139, figs. 26-31) has called a fungus found by him on *Chlamydomonas* in England *Rhizidium appendiculatum*, but, if the sequence of development described is correctly interpreted, it cannot be referred either to *Scherffeliomyces* or to *Rhizidium*.

CORALLIOCHYTRIUM Domján

Folia cryptogam., 2(1):22. 1936

(Figure 12 H-J, p. 244)

Thallus extramatrical, epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming the rudiment of the sporangium from the enlarged extramatrical part of the germ tube of the encysted zoospore, the endobiotic part forming a subsporangial apophysis from the base of which emerges a single short rhizoid bearing at its tip a complex of stubby, thick, branched digitations; sporangium inoperculate, epibiotic, sessile, the cyst of the zoospore attached to it directly or by a short tube, forming more than one discharge papilla; resting spore epibiotic, apparently asexually produced, borne within a structure formed like and resembling a sporangium, germination not observed.

On *Zygnema*.

The genus bears a marked similarity in its method of development to *Scherffeliomyces*. It differs, however, in the character of the haustorial system and the method of zoospore discharge (through several openings).

CORALLIOCHYTRIUM SCHERFFELII Domján

Folia cryptogam., 2 (1):22, pl. 1, figs. 5-12, 14-23, 27-35, 38-41, 47, 49. 1936

Sporangium sessile, somewhat irregularly angular-pyriform (polygonal in cross section at the base), the shape depending in part upon the number (from two to five) of broad very prominent elongate discharge papillae formed, 15.4-23.8 μ broad by 17.6-23.8 μ high (majority 22 μ in breadth), wall smooth, thick, colorless, bearing at the apex the cyst of the zoospore and its connective; subsporangial endobiotic apophysis bulbous, 3.3-4.4 μ in diameter, lateral walls thick, base generally thin-walled, the delicate basal rhizoid bearing distally the broad stubby digitations; zoospores spherical, 2.2 μ in diameter, with a colorless eccentric globule and a long flagellum, emerging singly through from two to five pores formed upon the deliquescence of the papillae; resting spore spherical, with a moderately thick colorless wall, 13.2 μ in diameter, contents with numerous small oil droplets, germination not observed.

On *Zygnema* sp., HUNGARY.**SUBFAM. ENTOPHYLYCTOIDEAE**

Sporangium endobiotic, resting spore endobiotic; vegetative system rhizoidal; zoospore cyst usually evanescent.

ENTOPHYLYCTIS FISCHER

Rabenhorst. Kryptogamen-Fl., 1 (4):114. 1892

(Figure 13, p. 252)

Thallus endobiotic, monocentric, eucarpic, consisting of the evanescent epibiotic cyst of the zoospore and the endobiotic rudiment of the sporangium or resting spore and a rhizoidal system arising from it; sporangium inoperculate, with a discharge tube the tip of which at least is extramatrical; zoospores posteriorly uniflagellate, with a single globule, formed within the sporangium, escaping upon the deliquescence of the tip of the discharge tube; resting spore thick-walled, endobiotic, borne like the sporangium, apparently asexually

formed, upon germination (*Entophysycis Vaucheriae*) forming zoospores in an extruded vesicle.

Primarily inhabitants of fresh-water green algae. Several species have been described by Němec (1912) as parasites of phanerogams.

There is some question at the moment as to the precise method of development of the thallus in *Entophysycis*. All the earlier investigators state that the rhizoids arise as outgrowths of the rudiment of the sporangium—the endobiotic part of the thallus first established. Karling (1931a), however, has observed in "*E. Cienkowskiana*" that the rudiments of the rhizoidal system are laid down first by the penetrating zoospore. By a subsequent enlargement of the more proximal part of the germ tube the incipient sporangium arises behind the point of origin of the primary branches of the rhizoids. This sequence of formation needs further confirmation of its occurrence in other species of *Entophysycis*. From analogy with *Diplophysycis* (see p. 261) it is possible that it is universal in the genus.

Germination of the resting spores has been observed apparently only by Fisch (1884a). In this process as it occurred in *Entophysycis Vaucheriae* the taking in of water caused the endospore to swell and to burst the exospore wall. In the extruded endospore the zoospores were formed after a period of pronounced cytoplasmic streaming. These zoospores, from Fisch's figure, varied greatly in size and did not fill the cavity of the extruded vesicle as one might suppose they would. The process, as described by Fisch, needs corroboration.

Specific concepts in *Entophysycis* are by no means clear, and considerable investigation will be necessary before they can be adequately defined. At present the characters most used to distinguish species are shape and size of the sporangium, number and, particularly, place of origin of the rhizoids on the sporangium, and host. Since, as Karling (1931a) aptly points out, very little is known concerning the range of variation of a single species under different conditions in diverse substrata and, as can be added, since little is known of the resting stage, no critical analysis of them can now be attempted.

KEY TO THE SPECIES OF ENTOPHLYCTIS

Epibiotic cyst persistent, functioning in the discharge of zoospores

Rhizoidal system limited, delicate; on chlamydomonads

E. apiculata, p. 253

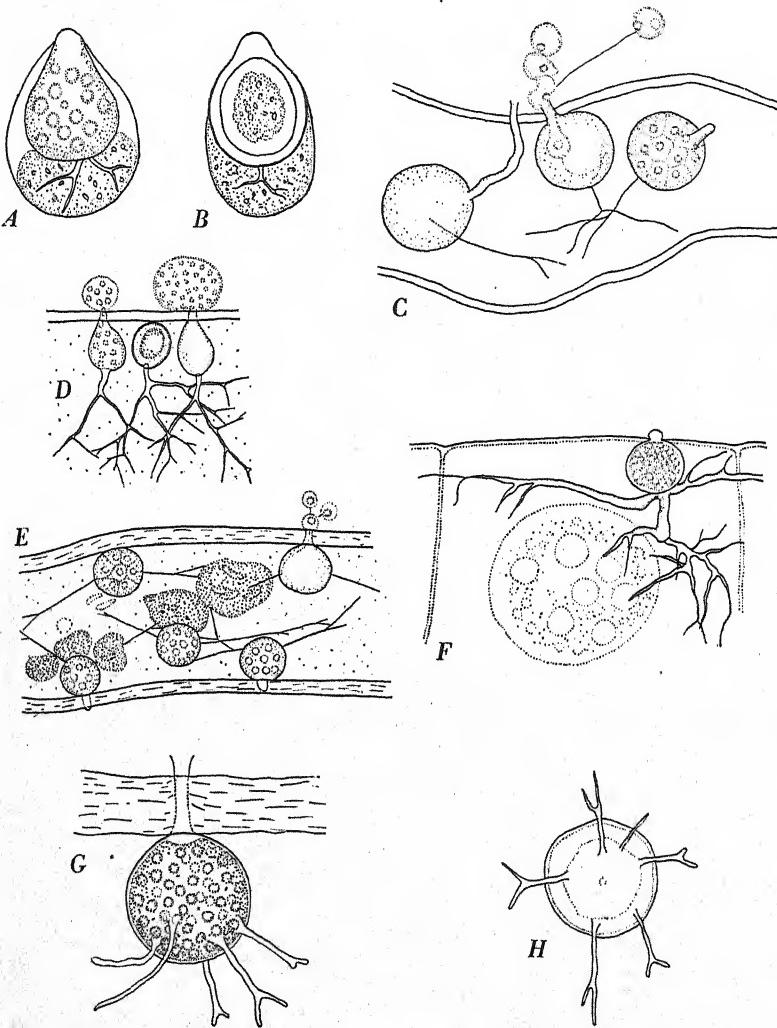


FIG. 13. Entophlyctoideae

A-B. Entophlyctis apiculata (Braun) Fischer ($\times 450$) in *Gloeococcus* (*Chlamydomonas* ?): *A*, habit of sporangial plant; *B*, resting spore. *C. Entophlyctis* (?) *Vaucheriae* (Fisch) Fischer ($\times 750$) in *Cladophora*. *D.* Discharging sporangia and a resting spore of *Entophlyctis Confervae-glomeratae* (Cienkowski) Sparrow ($\times 400$) in *Spirogyra*. *E. Entophlyctis* (?) *rhizina* (Schenk) Minden ($\times 400$) in *Vaucheria*. *F. Entophlyctis* *bulligera* (Zopf)

- Rhizoidal system extensive, coarse; on *Spirogyra* . *E. bulligera*, p. 254
 Epibiotic cyst not functional, evanescent
- Zoospores with an orange-colored globule *E. rhizina*, p. 255
- Zoospores with a colorless globule
- Rhizoids coarse, strongly dichotomously branched, main axes lateral; sporangium subspherical or oblong . *E. pygmaea*, p. 256
- Rhizoids delicate, regularly or irregularly branched
- Rhizoids arising in most cases from a single basal axis; sporangium spherical, broadly ellipsoidal, or pyriform; in green algae
- Sporangium predominantly spherical, basal axis delicate *E. Vaucheriae*, p. 257
- Sporangium predominantly spherical, broadly ellipsoidal, or somewhat pyriform, main axis relatively stout *E. Confervae-gloemeratae*, p. 258
- Rhizoids arising from three to twelve main axes; in Characeae *E. helioformis*, p. 259

ENTOPHYLYCTIS APICULATA (Braun) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):117. 1892

(Figure 13 A-B)

Chytridium apiculatum Braun, Monatsber. Berlin Akad., 1855:383; Abhandl. Berlin Akad., 1855:57, pl. 5, figs. 5-20. 1856.

Olpidium apiculatum (Braun) Rabenhorst, Flora Europaea algarum, 3: 283. 1868.

Rhizidium apiculatum (Braun) Zopf, Nova Acta Acad. Leop.-Carol., 47:207, pl. 21, figs. 21-31. 1884.

Sporangium broadly pyriform or nearly spherical, its papillate apiculus 3 μ long, piercing the host wall, main body resting between the retracted host contents and the wall, up to six sporangia in a cell, 11-13 μ in diameter, wall smooth, colorless; rhizoids imbedded in the host plasma, short, delicate, sparsely branched, arising from a short main axis; zoospores from three to twenty, small, spherical or ellipsoidal, with an eccentric colorless globule and a long flagellum, escaping upon the dissolution of the apex of the apiculus; resting

Fischer ($\times 270$) in *Spirogyra*; epibiotic knob is persistent case of zoospore. G-H. *Entophlyctis helioformis* (Dang.) Ramsbottom ($\times 750$) in *Nitella*: G, mature sporangium bearing stubby rhizoids; H, underside of empty sporangium showing attachment of stubby rhizoids.

(A-B, F, Zopf, 1884; D-E, Sparrow, 1936a)

spore spherical, subspherical, or ellipsoidal, with a thick colorless smooth wall, contents densely granular, rhizoidal system like that of the sporangium, germination not observed.

Parasitic in immobile and moving cells of *Gloeococcus* (*Chlamydomonas?*) *mucosus*, Braun (*loc. cit.*), *Chlamydomonas pulvisculus* (coll. Pringsheim), Braun (1856a:57), *Gloeocystis* or *Gloeococcus mucosus*, Kloss (in Braun, 1856b:588), *Gloeococcus* (?), Zopf (*loc. cit.*), GERMANY; *Gloeococcus mucosus*, Sorokin (1874b:10, pl. 1, figs. 11-43; 1883:32, fig. 36), RUSSIA; *Gloeococcus*, de Wildeman (1890:10), BELGIUM; *Chlamydomonas* sp., Constantineanu (1901:382), RUMANIA.

Sparrow (1936a:451, pl. 14, figs. 7-9) has tentatively referred a fungus on resting cells of *Euglena* sp. in England to this species. As he pointed out, however, since no rhizoids were observed in the dense contents the fungus might have been a species of *Olpidium*. Indeed, the same might be said of Braun's specimens. It was only after Zopf extracted the chlorophyll of his host plants that he was able to detect the rhizoids.

Zopf, to whom we owe most of our knowledge of the species, found it during February and March in several localities. It caused an epidemic of nearly three weeks' duration in one pond, where very few of the millions of algal cells escaped infection. He confirmed the observation of all investigators of the species, namely, that actively moving swarm cells of the alga were attacked by the fungous zoospores.

Braun states that the epibiotic cyst of the infecting zoospore and the germ tube are persistent in this species, the former producing the apiculus, the latter, the body of the sporangium. Zopf's figures bear out these observations.

ENTOPHYLYCTIS BULLIGERA (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):116. 1892

(Figure 13 F, p. 252)

Rhizidium bulligerum Zopf, Nova Acta Acad. Leop.-Carol., 47:195, pl. 18, figs. 5-8. 1884.

Sporangium spherical, variable in size, with an epibiotic knoblike or ovoid part—the body of the infecting zoospore—which functions as a discharge tube at maturity, wall slightly thickened, smooth, colorless; rhizoidal system extensive, branched, often passing through

several cells of the alga, arising from a single point on the under side of the sporangium or from numerous places on the lower half, rhizoids often becoming strongly expanded main axes where they join the sporangium; zoospores from thirty to forty in large sporangia, discharged through a pore formed in the epibiotic apiculus; resting spore not observed.

In moribund vegetative cells and gametangia of *Spirogyra crassa*, Zopf (*loc. cit.*), GERMANY; *Spirogyra crassa*, *Oedogonium sp.*, de Wildeman (1890:7; 1891:172), BELGIUM; *Spirogyra crassa*, Atkinson (1909a:338), UNITED STATES; *Oedogonium sp.*, Valkanov (1931a:363), BULGARIA; vegetative cells of *Zygnema* and *Mougeotia*, Domján (1936:46, pl. 1, figs. 71, 82-83), HUNGARY.

As in *Entophysycis apiculata*, the cyst of the infecting zoospore in this species is persistent and functions in spore discharge. Neither empty sporangia showing this pore nor zoospores were described by Zopf. Empty sporangia figured by Domján, however, bear out Zopf's contention that the apiculus functions as a discharge tube.

Valkanov gives the diameter of the sporangium as 17-18 μ ; Domján records the size as 10-15 \times 7.5-10 μ , with the knob 3.7-7.5 μ in diameter.

ENTOPHYCTIS RHIZINA (Schenk) Minden

Kryptogamenfl. Mark Brandenburg, 5:354. 1911 (1915)

Chytridium rhizinum Schenk, Verhandl. Phys.-Med. Gesell. Würzburg, A. F., 8:238, pl. 5, figs. 6-13. 1858.

Sporangium spherical or somewhat ovoid, 8-27 μ in diameter, wall smooth, usually double-contoured, forming a single extramatrical discharge tube (rarely two) 4-14 μ long by 1 μ in diameter; rhizoids arising from one or more places on the lower side of the sporangium, branched, somewhat stout, with a visible lumen as they approach the sporangium; zoospores spherical, 2 μ in diameter, with a reddish-yellow globule and a flagellum; resting spore not observed.

In *Vaucheria geminata*, *V. sessilis*, Schenk (*loc. cit.*), GERMANY; Voronichin (1920:10), RUSSIA.

Minden (*loc. cit.*) considers *Entophysycis Vaucheriae* (Fisch) Fischer synonymous with Schenk's species. The presence of a colored globule in the zoospore of Schenk's fungus (not mentioned

by Minden) is in itself sufficient to distinguish the two. Schenk's species bears a close resemblance to *Cladochytrium Nowakowskii* (see *C. replicatum*, p. 310), and it is not impossible that when the sporangia and rhizoids were crowded in the algal cell the turbinate cells were overlooked.

Though the rhizoids are said by Schenk to emerge from more than one place on the sporangium, all his figures except the immature stage in Figure 10 show a definite basal main axis. His statement that the flagellum of the zoospore is anterior during motility is probably erroneous, since even with the best modern optical equipment this structure can rarely be detected while rapidly vibrating.

Schenk believed his fungus was identical with "*Rhizidium*" *Confervae-gloemeratae* Cienkowski, differing only in the lack of amoeboid motion by the spores, their failure to form a motionless group at the orifice of the sporangium, and their not entering as a whole into the algal cell (probably an erroneous observation by Cienkowski). Cienkowski's fungus appears to form predominantly spherical rather than ovoid sporangia, the discharge tubes never extend an appreciable distance outside the algal wall, and the globule of the zoospore is colorless.

The species is reported as occurring in Bulgaria, in *Vaucheria sp.*, by Valkanov (1931a:363), and in Hungary by Domján (1936:46, pl. 1, fig. 137) (see also Moesz, 1938:71). Neither Valkanov nor Domján mentions a colored globule in the zoospore. A fungus closely resembling Schenk's but with colorless globules has been found in England (Sparrow, 1936a); see Figure 13 E, page 252.

ENTOPHYLYCTIS PYGMAEA (Serbinow), comb. nov.

Catenaria pygmaea Serbinow, Scripta Bot. Horti Univ. Imper. Petro., 24:161, pl. 3, figs. 1-15. 1907.

Sporangium endobiotic, single, subspherical or long-cylindrical with rounded ends, 17-26 μ long by 6-12 μ in diameter, terminal or intercalary, separated by cross walls from the rhizoidal system, with a single short papilla which penetrates the wall of the substratum; rhizoidal system strongly dichotomously branched, polyphagous, the main axis arising from one or opposite ends of the sporangium, broad and tubular, up to 3 μ in diameter, the branches rhizoidal; zoospores spherical, 1.5 μ in diameter, with a single globule, posteriorly uniflagellate, emerging upon the deliquescence of the papilla and forming

a temporary compact motionless mass at the orifice before assuming motility; resting spore borne like the sporangium, spherical, with a thickened colorless wall and a central oil globule, germination not observed.

Parasitic in *Mougeotia* sp., Serbinow (*loc. cit.*), FINLAND; saprophytic in *Mougeotia*, Sparrow, UNITED STATES (MICHIGAN).

The thallus of this organism is definitely monocentric and, so far as could be determined, the sporangium is inoperculate.

ENTOPHYLYCTIS VAUCHERIAE (Fisch) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):117. 1892

(Fig. 13 C, p. 252)

Rhizidium Vaucheriae Fisch, Sitzungsber. Phys.-Med. Soc. Erlangen, 16:55, pl. 1, figs. 10-23. 1884.

Sporangium spherical, with a beaklike or narrowly cylindrical apical discharge tube more or less prolonged extramatrically, wall smooth, colorless, thin or slightly thickened; rhizoids arising basally from a delicate central axis or occasionally from two places on the lower part of the body, delicate, fairly extensive, and much branched; zoospores relatively few, a large amount of contents usually remaining in the sporangium after their formation, spherical, with a centric or eccentric colorless globule and a short flagellum, discharge not described; resting spore endobiotic, thick-walled, the outer wall brown, the inner lustrous, contents finely granular, vacuolate, with a more or less large oil globule, germinating in the spring by the swelling of the endospore, which bursts the exospore, the former emerging as a subspherical structure within which are produced zoospores.

In *Vaucheria sessilis*, *Spirogyra* sp., Fisch (*loc. cit.*), GERMANY; alga (?), Petersen (1910:545), DENMARK; Sparrow, UNITED STATES (MICHIGAN).

Doubtfully distinct from *Entophlyctis Confervae-gloemeratae*. In certain figures the fungus appears polycentric, as in *Cladochytrium*. This is probably an error in observation due to several plants being superimposed. *E. Vaucheriae* is apparently the only species of the genus in which germination of the resting spore has been seen. *Rhizidium Spirogyrae* was the name given by Fisch to what was

probably the same fungus growing on *Spirogyra*. No description accompanied the name.

ENTOPHYLYCTIS CONFERVAE-GLOMERATAE (Cienkowski), comb. nov.

(Figure 13 D, p. 252)

Rhizidium Confervae-gloemeratae Cienkowski, Bot. Zeitung, 13:233, pl. 5 A, figs. 1-6 (not fig. 6c). 1857.

Rhizidium Cienkowskianum Zopf, Nova Acta Acad. Leop.-Carol., 47:196, pl. 17, figs. 14-24; pl. 18, figs. 1-4. 1884.

Entophlyctis Cienkowskiana (Zopf) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):118. 1892.

Sporangium spherical, broadly ellipsoidal, or somewhat pyriform, 5-25 μ in diameter, wall thin, smooth, colorless, discharge tube single (rarely two), narrowly cylindrical, straight or contorted, varying in length from a wartlike nearly sessile protuberance 3 μ long to several times the diameter of the sporangium; rhizoids branched, fairly extensive, predominantly arising from a somewhat prolonged basal axis (occasionally two), sometimes arising from several places on the lower part of the sporangium; zoospores spherical, 2.5-5 μ in diameter, with a strongly refractive colorless globule and a long flagellum, emerging singly and somewhat amoeboidly from the orifice of the discharge tube and resting for a time (or clustering temporarily) before swimming away; resting spore formed and borne like the sporangium, spherical, with a thick, faint-golden-brown wall, contents with a large oil globule filling the lumen of the spore, germination not observed.

In *Cladophora glomerata*, Cienkowski (*loc. cit.*), ITALY (?); dead or moribund *Cladophora*, Zopf (*loc. cit.*), Minden (1915:357), GERMANY; *Cladophora glomerata*, Sorokin (1883:34, fig. 41), EUROPEAN RUSSIA, ASIATIC RUSSIA; *Cladophora* sp., Dangeard (1886a:293), de Wildeman (1894:158), FRANCE; *Spirogyra crassa*, de Wildeman (1890:7), BELGIUM; *Cladophora*, Karling (1931a:443, pl. 35-38), Sparrow (1933c:524), UNITED STATES; *Spirogyra* sp., Sparrow (1936a:452, pl. 14, figs. 13-17), ENGLAND.

As understood here, this collective species includes all forms with smooth-walled resting spores and spherical, broadly ellipsoidal, or somewhat pyriform sporangia bearing rhizoids which emerge typically from a main basal axis or less typically from several axes formed on

the lower half of the sporangium. Dangeard (*loc. cit.*) attempted to distinguish it from *Entophyscyltis helioformis* by the smaller number of rhizoids localized at the base of the sporangium. Such a localization is apparent in most specimens but not in all. This is at variance with Zopf's statement that the rhizoids arise mostly from all sides of the sporangium. It is possible that it will be better eventually to segregate his species from the present one. Typical of the species as here understood are the figures of Cienkowski (*loc. cit.*), Karling (*loc. cit.*), and Sparrow (1936a: pl. 14, figs. 13-17). With this interpretation of the species, *E. Vaucheriae* is scarcely distinct from *E. Confervae-globulatae* save for the difference in host plant. It is probable that when more is known about the resting stages of these fungi sharper lines of specific differentiation will be revealed than are apparent at the moment.

The fungus in *Vaucheria* from England tentatively described as *Entophyscyltis Confervae* by Sparrow (1936a: pl. 14, fig. 18), with spherical sporangia and delicate isodiametric rhizoids arising laterally or nearly basally on the sporangium, is distinct from this species. Since the resting stage was not found, however, it is thought best to leave it unnamed. It resembles the fungus called *E. rhizina* by Domján (1936:46, pl. 1, fig. 137) (see Fig. 13 E, p. 252).

ENTOPHYLYCTIS HELIOFORMIS (Dang.) Ramsbottom

Trans. Brit. Mycol. Soc., 5:318. 1915

(Figure 13 G-H, p. 252)

Chytridium helioformis Dangeard, Bull. Soc. Bot. France, 33:356. 1886;
Ann. Sci. Nat. Bot., VII, 4:293. 1886.

Chytridium heliomorphum Dangeard, Journ. de Botanique, 2:143, pl. 5,
figs. 19-23. 1888.

Entophyscyltis heliomorpha (Dang.) Fischer, Rabenhorst. Kryptogamen-Fl.,
1 (4):118. 1892.

Sporangium spherical or ovoid, 6-40 μ in diameter, wall smooth, colorless, somewhat thickened, discharge tube cylindrical, of variable length; rhizoids profusely (?) branched, arising from three to twelve main axes formed at any place on the sporangium; zoospores spherical, 3-4 μ in diameter, with a conspicuous centric or eccentric colorless globule and a long flagellum, escaping individually upon the rupturing of the tip of the discharge tube, movement swimming with axial rotation, or amoeboid; resting spore borne like the sporangium,

spherical, subspherical, or broadly ovoid, 8–24 μ in diameter, with a double wall, the outer thicker than the inner, contents yellowish, with numerous oil globules, germination not observed.

Saprophytic in *Nitella tenuissima*, *Vaucheria* sp., *Chara* sp., Dangeard (*loc. cit.*), FRANCE; *Chara* spp., *Nitella* spp., Karling (1928a:32, pl. 1, figs. 1–35), *Chara* sp., *Nitella tenuissima* (?), Sparrow (MICHIGAN), UNITED STATES.

The most ubiquitous member of the genus. It can be found in abundance in dead plants of *Chara* and *Nitella*. Karling, who has studied the development of the species (*loc. cit.*), has reported (1931a:443) negative results in his attempts to grow the fungus on moribund and dead sterile internodes of *Chara* and *Nitella*, filaments of *Spirogyra*, *Vaucheria*, *Oedogonium*, *Mougeotia*, and *Hydrodictyon*.

Although the rhizoids are said by some investigators to be extensive and profusely branched, in the Michigan material they were for the most part as Dangeard figured them, relatively short and once-branched.

The change in specific name from the Greek-Latin hybrid *helioformis* to *heliomorphum* was made by Dangeard without explanation.

IMPERFECTLY KNOWN SPECIES OF ENTOPHLYCTIS

? ENTOPHLYCTIS CHARACEARUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 20:131, pl. 12, figs. 1–10. 1896

Sporangium unknown; resting spore, spherical, ellipsoidal, or irregularly polygonal, 17–25 μ in diameter, with a thick smooth brownish wall; rhizoids much branched, generally arising from two stout main axes (occasionally one); germination not observed.

In oögonia of Characeae, SWITZERLAND.

The resting spores are certainly those of some chytrid, but until the sporangial stage is observed, it is difficult to say to which of several genera the fungus belongs.

? ENTOPHLYCTIS MAXIMA Dangeard

Le Botaniste, 24:242, pl. 24, figs. 4–5. 1932

Sporangium very broadly pyriform, 40 μ in diameter, with a broad apical papilla, 5–15 μ in diameter, which just pierces the algal wall;

rhizoids branched, arising from as many as three main axes on the lower half of the sporangium; zoospores and resting spore not observed.

In *Cladophora glomerata*, FRANCE.

Karling (1937a) considers this incompletely known form to be synonymous with *Endochytrium operculatum*.

? ENTOPHLYCTIS TETRASPORA (Sorokin) de Wildeman

Bull. Soc. Roy. Bot. Belg. (Mém.), 35:51. 1896.

Rhizidium tetrasporum Sorokin, Arch. Bot. Nord France, 2:35, fig. 42. 1883 (separate).¹

Sporangium pyriform, wall smooth, thin, colorless, with a short discharge tube which just pierces the wall of the alga; rhizoids short, apparently unbranched, forming a cluster at the base of the sporangium; zoospores four, spherical, with a short flagellum and a colorless eccentric globule; resting spore not observed.

In *Rhynchonema* (*Spirogyra?*) sp., RUSSIA.

The validity of the species has been questioned by Fischer and Minden. Sorokin's figure shows two empty sporangia (one with three zoospores near the orifice) and another in which four zoospores occupy only a small part of the available space. It is possible that the sporangium on which the four-spored character was based was already partly emptied.

? ENTOPHLYCTIS WORONICHINII Jaczewski

Opredelitel gribov.... I. Fikomitsety, p. 44. 1931

Sporangium of irregular shape and 19.8–13.7 μ in diameter or rounded and 10–11 μ in diameter, wall of two layers, colorless, 2–4 μ thick.

In zoospores of *Vaucheria sessilis*, *V. geminata*, RUSSIA.

DIPLOPHLYCTIS SCHROETER

Engler and Prantl, Natürlichen Pflanzenfam., 1(1):78. 1892 (1893)

(Figure 14, p. 263)

Thallus endobiotic, monocentric, eucarpic, consisting of the rudiment of the sporangium, an apophysis, and an extensive branched

¹ See also *Revue Mycologique*, 11:137, pl. 80, fig. 98. 1889.

rhizoidal system, the cyst of the infecting zoospore evanescent; sporangium inoperculate, with a discharge tube and an apophysis, zoospores posteriorly uniflagellate, with a single globule, fully formed within the sporangium, emerging through a pore produced at the tip of the discharge tube; resting spore thick-walled, borne like the sporangium, upon germination functioning either as a sporangium or a prosporangium.

Species of *Diplophlyctis* are primarily habitants of moribund and dead members of the Characeae and, less often, the Chlorophyceae. Indeed, it is difficult to find old plants of *Nitella* and *Chara* in which one species, *D. intestina*, is not present in abundance. *D. laevis* has thus far been found in nature only in *Cladophora*.

As indicated in the diagnosis, two methods of resting spore germination have been described in the literature. Zopf (1884:195) states that in *Diplophlyctis intestina* the resting structure becomes transformed into a sporangium and produces a discharge tube through which the zoospores emerge. Karling (1936b:469), on the other hand, who has observed many instances of germination in this same species, states that the contents emerge through a pore and form a thin-walled zoosporangium sessile to the thick-walled structure. Germination has not as yet been witnessed in *D. laevis*.

KEY TO THE SPECIES OF DIPLOPHLYCTIS

- Sporangium predominantly spherical, subspherical, or ellipsoidal,
apophysis appearing basal; resting spore spiny *D. intestina*, p. 262
Sporangium predominantly broadly or irregularly pyriform, apophysis generally appearing lateral; resting spore smooth *D. laevis*, p. 265

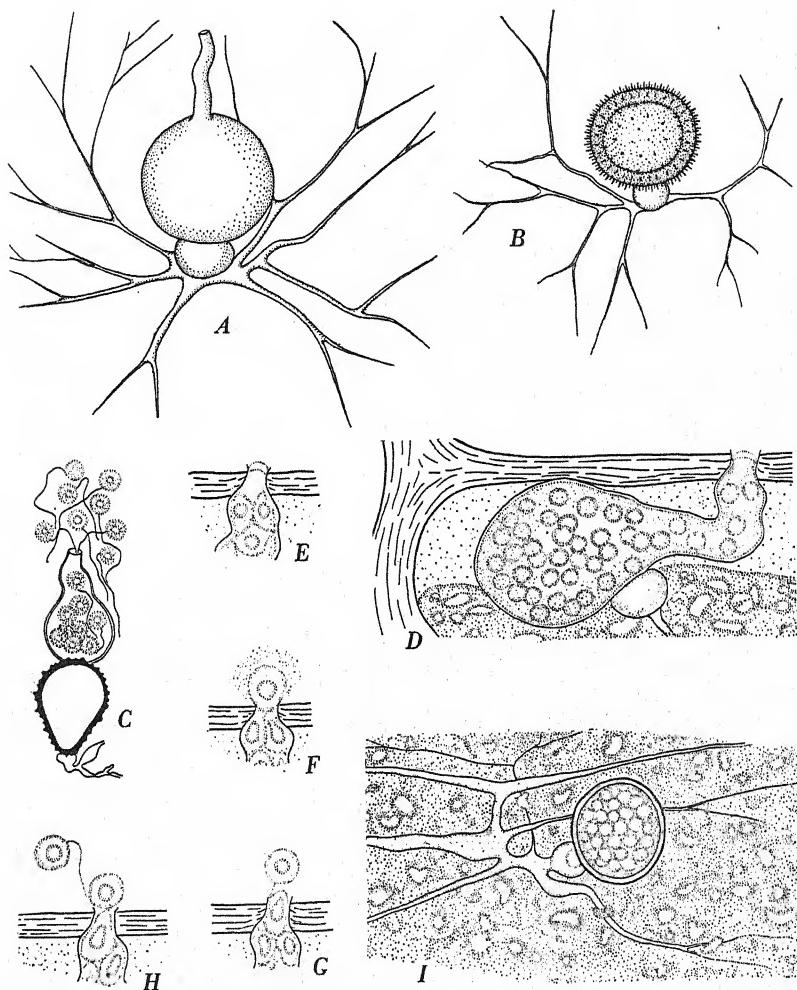
DIPLOPHLYCTIS INTESTINA (Schenk) Schroeter

Engler and Prantl, Natürlichen Pflanzenfam., 1 (1):78. 1892

(Figure 14 A-C)

Rhizidium intestinalum Schenk, pro parte, Ueber das Vorkommen contractiler Zellen im Pflanzenreiche, p. 5, figs. 1-9. Würzburg, 1858.
Entophyscites intestinalis (Schenk) Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4):116. 1892.

Sporangium predominantly spherical, subspherical, pyriform, or obliquely ellipsoidal, occasionally somewhat cylindrical, clavate, or irregular, variable in size, up to 80 μ or more in diameter, wall

FIG. 14. *Diplophlyctis*

A-C. *Diplophlyctis intestina* (Schenk) Schroeter ($\times 670$) in *Nitella*: A, empty apophysate sporangium with discharge tube; B, spiny resting spore; C, discharging sporangium formed at germination of resting spore. D-I. *Diplophlyctis laevis* Sparrow ($\times 750$) in *Cladophora*: D, mature sporangium with discharge tube opening on outside surface of algal wall; E-H, successive stages in discharge of zoospores; I, resting spore.

(A-B, Sparrow, 1932b; C, Karling, 1936b; D-I, Sparrow, 1939a)

thin, smooth, colorless, discharge tube generally single, cylindrical, slightly tapering distally, of variable length, apophysis appearing basal, variable in shape and size, usually spherical, subspherical, or pyriform and 3–6 μ in diameter; rhizoids richly branched, extensive, up to 400 μ in length, ordinarily arising from a single short basal axis, the main branches stout, tips delicate; zoospores variable in number, spherical or somewhat ovoid, 4–6 μ in diameter, with a large, colorless, eccentric globule and a long flagellum, emerging individually through a pore at the tip of the discharge tube and swimming directly away or forming a temporary motionless mass at the orifice before escape, movement swimming or amoeboid; resting spore spherical, subspherical, or broadly ellipsoidal, variable in size, up to 22 \times 28 μ , wall thick, yellowish or brown, the outer surface covered by minute short sharp spines, apophysis and rhizoidal system like those of the sporangium, upon germination either forming a tube and functioning as a zoosporangium or becoming a prosporangium and producing a sessile thin-walled zoosporangium.

Saprophytic or weakly parasitic in dead or moribund internodal cells of *Nitella flexilis*, Schenk (*loc. cit.*), *N. mucronata*, *N. flexilis*, Zopf (1884:191, pl. 19, figs. 1–15), GERMANY; *Nitella tenuissima*, *Chara polycaanthum*, Dangeard (1886a:296, pl. 13, figs. 20–23; 1890–91b:91, pl. 4, figs. 13–18), FRANCE; "Characeae," Petersen (1909: 413; 1910:548), DENMARK; *Chara coronata*, *C. fragilis*, *C. delicatula*, *Nitella flexilis*, *N. glomerulifera*, *Lamprothamnus alopecuroides*, *Lychnothamnus barbatus*, Karling (1928b:204, text figs. 1–2, pl. 14; 1930: 770, text figs. 1–2, pls. 46–49; 1936b:469, text figs. 1–8), *Nitella flexilis*, Sparrow (1932b:283, figs. 2 e, j; 1936d:321, figs. 1–2), UNITED STATES.

In spite of the fact that this species has been the object of a considerable amount of study there remain certain features in need of further clarification.

Zopf (*loc. cit.*) and Karling (1928b) showed clearly that in the development of the thallus the rudiment of the sporangium was the first structure laid down by the emerged plasma of the infecting zoospore. The apophysis was then formed as an outgrowth of this rudiment, followed by the rhizoids. Karling (1930) later asserted that the rudiments of the rhizoidal system were the primary elements of the young thallus, and that then the rudiment of the sporangium

and lastly the apophysis were laid down. This sequence was confirmed by Sparrow (1936d).

The most pertinent question remaining in the life history of the fungus is whether or not the formation of the resting spores, which in this chytrid are always produced in abundance, is preceded by any type of sexual process. Dangeard (1890-91b) suggested that certain abnormal swellings on several resting stages he observed might be antheridia, but he did not stress their male function. The endogenous method of resting-spore formation involving separation of the contents into ooplasm and periplasm, also described by Dangeard, has not been confirmed by later investigations. Sparrow (1936d) has recently presented evidence for a sexual process essentially like that found in *Siphonaria*, *Rhizoclostratum*, and *Astero-phlyctis*. Small undeveloped thalli 10 μ high by 5 μ in diameter, with a small rhizoidal system, were found almost constantly associated with the resting spores. In particularly good specimens it could be seen that there was a definite connection between the rhizoidal systems of the two types of structures. Anastomosis was usually achieved by the rhizoid of the larger body, into which the contents of the smaller presumably passed. Sparrow's observations seemed to indicate that connection of the two and transference of material took place at a very early stage in thallus development. Owing to the small size of the structures involved, however, further researches are needed to confirm these observations.

Dangeard (1886a) noted that the sporangium alone, or the sporangium and the apophysis, may occasionally be epibiotic.

DIPLOPHLYCTIS LAEVIS Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:296. 1937; Papers Mich. Acad. Sci., Arts, Letters, 24 (1938), Pt. I:121, pl. 1, figs. 1-14. 1939

(Figure 14 D-I, p. 263)

Sporangium broadly or irregularly pyriform, 20-35 μ long by 13-35 μ in diameter at the base, with a subspherical, subsporangial, or lateral apophysis 4-5 μ in diameter, from which one or several stout branching rhizoids emerge, discharge tube broad, tapering, of variable length (up to 50 μ), its tip penetrating the host wall and generally protruding only slightly beyond it; zoospores spherical, 7 μ in diameter, with a single colorless oil globule 3 μ in diameter and a posterior flagellum 30 μ long; resting spore spherical or ellipsoidal, 11-18 \times

12–18 μ , with a smooth wall about 2 μ thick surrounding the contents, in which are many oil globules of approximately the same size, and a spherical apophysis 5–7 μ in diameter, germination not observed.

Saprophytic in cells of *Cladophora sp.*, UNITED STATES.

Variations in the shape of the sporangium and the often lateral position of the apophysis may possibly be due to restrictions of space imposed upon the fungus by the relatively narrow *Cladophora* cells. At maturity a cross wall is always formed between the sporangium and the apophysis.

Because of the predominantly pyriform sporangia (see Fig. 14 D, p. 263) and the variable position of the apophysis the aspect of the sporangial stage is quite different from that of *Diplophlyctis intestina*, and the two could not be confused even if resting spores were not formed.

MITOCHYTRIDIUM DANGEARD

Bull. Soc. Mycol. France, 27:202. 1911

(Figure 15 C, p. 268)

Thallus endobiotic, eucarpic, monocentric, consisting of a broad, cylindrical, and unbranched, branched, or irregularly lobate tube, the rudiment of the zoosporangium, from which arise one or more delicate axes which become divided distally into rhizoids, wall giving a cellulose reaction with chloriodide of zinc; sporangium inoperculate, formed from the tubular part of the thallus which is cut off by cross walls from the rhizoids; zoospores posteriorly uniflagellate, with a single globule, completely formed within the sporangium and escaping successively to the outside by one or more short tubes which penetrate the wall of the substratum; resting spore (?) endobiotic, with rhizoids, apparently asexually formed, germination not observed.

A monotypic genus, parasitic in desmids.

The precise method of development is not known with absolute certainty. The observations of Couch (1935c:293) indicate that the tubular part of the thallus—the rudiment of the future sporangium—is laid down before the purely vegetative part, that is, the rhizoids,

and soon becomes separated from the more or less elongated penetration tube.

Both Dangeard and Couch state that thick-walled endobiotic resting bodies are formed. These appear, in contrast to the monocentric sporangial stage, to be polycentric in origin, several being produced on a common rhizoidal system. If both investigators did not, in fact, have a mixture of *Mitochytridium* and *Catenaria* (see Couch, *op. cit.*, pl. 62, fig. 9), this is an extraordinary condition, not found in any other of the chytrids except *Physoderma* and *Urophlyctis*.

The genus differs from *Catenaria* chiefly in the fact that the thallus gives rise to a single sporangium. It appears more nearly related to *Entophyslyctis* than to any of the Cladophytriaceae, where it is usually placed.

MITOCHYTRIDIUM RAMOSUM Dangeard

Bull. Soc. Mycol. France, 27:202, fig. 1. 1911

Sporangium nearly isodiametric throughout, straight and unbranched or branched, twisted, and bearing short lobulations, up to $660\ \mu$ in length, $10-30\ \mu$ in diameter, wall somewhat thick, smooth, colorless; rhizoids extensive, branched, arising from main axes generally formed at the extremities of the sporangial rudiment; zoospores somewhat ovoid or spherical, $4-5\ \mu$ in diameter, with a colorless eccentric globule and a long flagellum, escaping successively through one or more short discharge tubes which penetrate the wall of the alga but do not extend beyond it; resting spores (?) spherical or elongated, thick-walled, $12-25\ \mu$ in diameter, several formed on the same thallus and connected to it by one or more rhizoids, the bases of which persist as spiny or blunt protuberances after the spore is free from the thallus, germination not observed.

Parasitic on *Docidium Ehrenbergii*, Dangeard (*loc. cit.*), FRANCE; *Docidium* sp., Couch (1935c:293, pl. 62, figs. 1-12), UNITED STATES.

Couch has noted that the thallus varies from a short unbranched structure to a long branched twisted body that may extend throughout the entire length of the desmid cell ($660\ \mu$). More than one thallus may be formed in a single host cell. Couch believes that the fungus is closely allied to the polycentric *Catenaria*. It appears, however, to be an *Entophyslyctis*-like organism with a tubular reproductive rudiment.

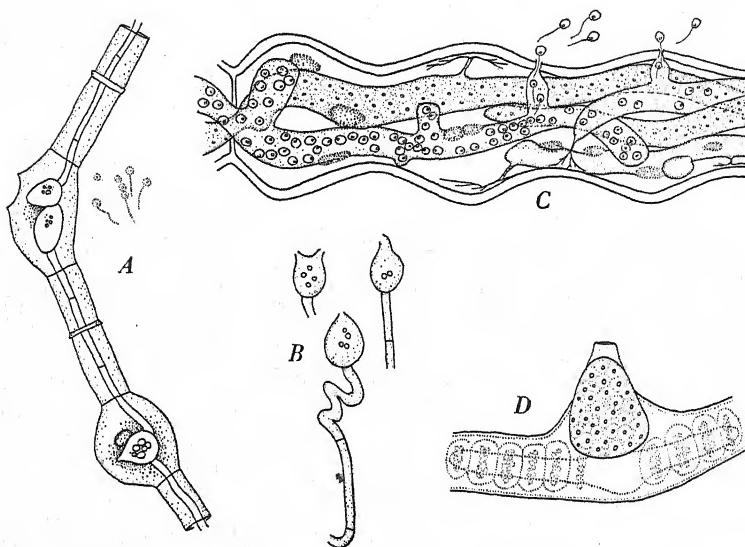


FIG. 15. Entophlyctoideae

A-B. Aphanistis Oedogoniorum Sorokin ($\times 450$) in *Oedogonium sp.*: A, plants bearing sporangia in oögonia of host; a group of zoospores is shown to right of filament; B, different shapes assumed by zoosporangia. C. *Mitocytridium ramosum* Dangeard in *Docium sp.*, portion of desmid cell with parts of several sporangia. D. *Rhizosiphon crassum* Scherffel ($\times 750$) in filament of *Filarszkya sp.*, mature sporangium with already opened discharge tube, resting laterally on broad prosporangium.

(A-B, Sorokin, 1883; C, after Couch, 1935c; D, Scherffel, 1926a)

RHIZOSIPHON SCHERFFEL

Arch. Protistenk., 54:189. 1926

(Figure 15 D)

Thallus endobiotic, monocentric, eucarpic, polyphagous, consisting of a central structure—the rudiment of the prosporangium—from which emerge on opposite sides two broad isodiametric unbranched hypha-like vegetative structures (occasionally one); sporangium inoperculate, partly or wholly extramatrical, formed as an outgrowth of the prosporangium; zoospores posteriorly uniflagellate, with a single globule, fully formed in the sporangium, escaping through a short discharge tube; resting spore thick-walled, with

many globules, endobiotic, without a vegetative system, upon germination functioning as a prosporangium.

A monotypic genus, parasitic on the blue-green alga *Filarszkya*.

RHIZOSIPHON CRASSUM Scherffel

Arch. Protistenk., 54:189, pl. 9, figs. 41-55. 1926

Prosporangium broadly fusiform when intercalary, somewhat clavate when terminal; sporangium broadly and somewhat irregularly pyriform, 14-18 μ in diameter, arising laterally from an intercalary prosporangium or apically from a terminal one, with a broad conical prominent discharge tube, wall thin, smooth, colorless; zoospores spherical, 3 μ in diameter, with an inconspicuous faintly refractive basal globule 1 μ in diameter or with several highly refractive granules, with a posterior flagellum 18 μ long, escaping singly and amoeboidly through the open apex of the discharge tube and remaining for a time near the orifice before darting away; resting spore round-oblong, broadly fusiform and 10-12 \times 15-25 μ , or nearly spherical (ellipsoidal) and 6-12 \times 8-15 μ , wall double-contoured, smooth, colorless, contents with many colorless coarse highly refractive globules, upon germination forming a narrowly pyriform sessile sporangium with a smooth colorless thin wall.

Parasitic on *Filarszkya* sp., HUNGARY.

The fungus was notable in having a remarkable effect on the coloration of the algal filament (see under "Parasitism," p. 70). Another unusual feature was the production of a strongly vacuolate foamy stage in the sporangium preceding zoospore formation, reminiscent of a condition found in the *Saprolegniales*.

Scherffel considers that, in spite of the hypha-like nature of the vegetative system, the fungus is a chytrid allied to *Polyphagus* and *Saccommyes*. In all three genera the sporangium arises as an outgrowth of a prosporangium. *Rhizosiphon*, however, differs from these in the formation of a discharge tube and an endobiotic, apparently asexually formed, resting spore.

APHANISTIS SOROKIN

Arch. Bot. Nord France, 2:35. 1883 (separate)

(Figure 15 A-B)

Thallus endobiotic, monocentric, polyphagous, eucarpic, sterile part consisting of a branched or unbranched isodiametric septate

filament; sporangium inoperculate, terminal, separated by a cross wall from the vegetative part of the thallus, with or without one or more discharge tubes; zoospores posteriorly uniflagellate, with a single globule, escaping after the deliquescence of one or more papillae; resting spore not observed.

On *Oedogonium*.

Fischer, who put the genus in the Hypochytriaceae, considered it too poorly known to place taxonomically, and in this Minden concurred. It seems likely that the presence of a septate "mycelium" bearing a zoosporangium which formed posteriorly uniflagellate zoospores was too bizarre to be acceptable to these monographers. The genus, though unusual, is adequately described and leaves no doubt as to just what type of organism Sorokin saw. A somewhat similar thallus is found in *Coenomyces*.

APHANISTIS OEDOGONIORUM Sorokin

Arch. Bot. Nord France, 2:35, fig. 43 a-d. 1883 (separate)¹
(Figure 15 A-B, p. 268)

Sporangium formed only in the oögonium of the alga, at first ovoid, later nearly spherical, with one or two (opposite) apical papillae which may be formed on more or less prolonged discharge tubes that are pointed toward the oögonial opening; vegetative system isodiametric, simple or branched, the septations occurring at relatively long intervals; resting stage not observed.

In filaments and oögonia of *Oedogonium* sp., ASIATIC RUSSIA, EUROPEAN RUSSIA.

As in *Rhizophyllum decipiens*, the fertilization pore of the oögonium was utilized for the setting free of the zoospores of the fungus into the outside medium.

IMPERFECTLY KNOWN SPECIES OF APHANISTIS

? APHANISTIS (?) PELLUCIDA Sorokin

Arch. Bot. Nord France, 2:36, fig. 44. 1883 (separate)²

Sporangium terminal, ellipsoidal, with a sharp lateral beaklike discharge tube; vegetative system rudimentary, the few cells bearing

¹ See also *Revue Mycologique*, 11:137, pl. 79, figs. 79-83, 85. 1889.

² See also *ibid.*, pl. 79, fig. 84.

lateral protrusions of variable extent; zoospores not observed; resting spore not observed.

In young plants of *Oedogonium sp.*, ASIATIC RUSSIA.

IMPERFECTLY KNOWN GENUS OF THE PHLYCTIDIACEAE

? ACHLYELLA LAGERHEIM

Hedwigia, 29:144. 1890

(Figure 10 F, p. 152)

Thallus epi- and endobiotic, monocentric, the epibiotic part consisting of the rudiment of the sporangium, the endobiotic part a broad rounded haustorium without rhizoids; sporangium inoperculate; zoospores emerging as nonflagellate individuals, encysting in a group at the orifice of the sporangium, emerging from the cyst through a minute pore, flagellation of the motile spores unknown; resting spore not observed.

On pollen of *Typha*.

Because of the lack of information on the development of the thallus and on the flagellation of the spore the relation of the genus to the chytrids is problematic.

? ACHLYELLA FLAHAULTII Lagerheim

Hedwigia, 29:144, pl. 2, figs. 5-7. 1890

Sporangium inoperculate, sessile, narrowly pyriform, with a somewhat prolonged erect or bent apex, wall slightly thickened, colorless, smooth; haustorium broad, knoblike, thin-walled; zoospores discharged through a pore formed at the apex of the sporangium, cysts spherical; otherwise unknown.

On pollen of *Typha*, FRANCE.

RHIZIDIACEAE

Thallus predominantly interbiotic, monocentric, eucarpic, consisting of a well-developed usually extensive rhizoidal system, the tips of which at least are endobiotic, and a reproductive rudiment

which is converted into a sporangium, prosporangium, gametangium, or resting spore; sporangium inoperculate; zoospores posteriorly uniflagellate (except where aplanospores are formed), with a single globule; resting spore asexually formed or sexually by fusion of iso- or anisogamous aplanogametes which are never liberated into the outside medium, upon germination functioning as a sporangium or a prosporangium.

Characterized as a group by the formation of an extensive richly branched often polyphagous rhizoidal system and a reproductive rudiment which ordinarily is not intimately connected with the substratum. The family includes many of the most interesting and bizarre parasites of fresh-water algae, as well as the curious group of species inhabiting the exuviae of aquatic insects. In some forms the zoospore bears a brightly colored globule. Where sexuality occurs, it takes place by the fusion of aplanogametes. The sexual process in *Polyphagus* (see under "Sexual Reproduction," p. 49) has been studied both morphologically and cytologically and is perhaps the best known among the chytrids. The type involving anastomosis of the rhizoids, as found in *Siphonaria*, is less well understood.

KEY TO THE SUBFAMILIES AND GENERA OF THE RHIZIDIACEAE

- Body of the encysted zoospore or aplanospore forming the rudiment of the sporangium; sexuality, where known, by conjugation of thalli by means of rhizoidal anastomosis
- Rhizoids arising from the body of the sporangium or from a somewhat clavate main axis; resting spore apparently asexually formed Subfamily RHIZIDIORIDEAE, p. 273
- Vegetative system branched or unbranched, arising from one place on the sporangium
- Vegetative system consisting of an unbranched double-contoured tube, aplanospores formed SPOROPHYLYCTIDIUM, p. 274
- Vegetative system consisting of branched rhizoids arising from a more or less prolonged main axis, zoospores formed RHIZIDIUM, p. 275
- Vegetative system arising from more than one place on the sporangium
- Zoospores after discharge eventually leaving the vicinity of the sporangium as individuals RHIZOPHYLYCTIS, p. 281
- Zoospores discharged as a free-swimming aggregate which moves away from the vicinity of the sporangium and

- disassociates into successively smaller groups and, ultimately, into individuals *NOWAKOWSKIA*, p. 288
- Rhizoids arising from a subsporangial apophysis; resting spore formed by conjugation of thalli by means of rhizoidal anastomosis Subfamily *OBELIDIOIDEAE*, p. 289
- Lower part of the sporangium thickened to form a cuplike or funnel-like base, apophysis inconspicuous, discharge pore usually lateral or subapical *OBELIDIUM*, p. 289
- Lower part of the sporangium not differentiated from the remainder, apophysis usually conspicuous, discharge pore usually basal
- Rhizoids delicate, wide-lumened only near the apophysis, if at all
- Sporangium and resting spore spherical or subspherical
RHIZOCLOSMATIUM, p. 291
- Sporangium and resting spore because of the formation of prominent irregularly placed outgrowths appearing somewhat stellate *ASTEROPHYCTIS*, p. 294
- Rhizoids coarse, wide-lumened throughout, becoming delicate only at the extremities *SIPHONARIA*, p. 296
- Body of the encysted zoospore forming the rudiment of a prosporangium or a germ tube which expands in part to produce a prosporangium; resting spore resulting from the conjugation either of adnate thalli, in which case it is formed in the receptive thallus, or of thalli joined by a tube, in which case it is formed in the tube Subfamily *POLYPHAGOIDEAE*, p. 297
- Body of the encysted zoospore enlarging to form the rudiment of the prosporangium
- Zoospores escaping from the sporangium through an apical orifice as free-swimming bodies; resting spore formed in the tip of the conjugation tube of the receptive thallus
POLYPHAGUS, p. 297
- Zoospores escaping from the sporangium through a subapical or lateral orifice as nonmotile bodies (aplanospores) or germinating in the sporangium; resting spore formed by the receptive thallus, conjugating thalli adnate
SPOROPHYCTIS, p. 301
- Body of the encysted zoospore producing a germ tube, part of which expands to form the prosporangium *ENDOCOENOBIUM*, p. 303

SUBFAM. *RHIZIDIOIDEAE*

Reproductive rudiment formed from the body of the encysted zoospore or aplanospore; rhizoids arising directly from the body of the

sporangium or from a single main axis; resting spore apparently asexually formed.

SPOROPHYCTIDIUM SPARROW

Trans. Brit. Mycol. Soc., 18:217. 1933; 21:147. 1938

(Figure 16 H, p. 277)

Thallus monocentric, eucarpic, consisting of a sporangial rudiment (the body of the encysted zoospore) and a single unbranched nearly isodiametric tube, the tip of which is endobiotic; sporangium inoperculate, formed from the sporangial rudiment, spores (aplanospores) produced in the sporangium, at maturity liberated upon the formation of one or more discharge papillae, devoid of a flagellum; resting spore not known with certainty.

So far as is known, this is a monotypic genus living on fresh-water green algae.

Sporophlyctidium closely resembles *Sporophlyctis* in its main features. The relationship of the parasite to the alga is similar in the two fungi, as is the shape of the sporangium, the position of the discharge pore, and the nonflagellate zoospore. In *Sporophlyctidium*, however, the structure which makes contact with the host cell is never branched or rhizoidal, but unbranched and "inflated" (broad). Further, the zoospores of *Sporophlyctidium* are not formed in a vesicle (sporangium) extruded from the sporangium, but rather are segmented within the latter body and discharged individually. New investigations will be necessary before it can be said with absolute certainty that the resting spores found in the same material as the sporangia belong to the species.

SPOROPHYCTIDIUM AFRICANUM Sparrow

Trans. Brit. Mycol. Soc., 18:217. 1933; 21:147, fig. 1 a-f. 1938

Sporangium narrowly oboviform, smooth-walled, colorless, the narrower end continuous with the unbranched germ tube, 5 μ long by 3.5-4 μ in diameter, forming a single subapical pore through which the spherical aplanospores, 2 μ in diameter, with a single globule, are extruded; resting spore (?) similar in shape to the sporangium, 7 μ long by 4 μ in diameter, with a spherical companion cell 3 μ in diameter; germination not observed.

Parasitic on *Protoderma* sp., coll. E. F. Warburg, NORTH AFRICA (TANGIER).

RHIZIDIUM BRAUN

Monatsber. Berlin Akad., 1856:591; Flora, 14:599. 1856
(Figure 16 E-G, I-J, p. 277)

Thallus monocentric, eucarpic, consisting of a sporangial rudiment (the body of the encysted zoospore) and a broad main rhizoidal axis which bears secondary branches; zoosporangium inoperculate, formed from the sporangial rudiment, zoospores posteriorly uniflagellate, with a single globule, emerging imbedded in slime or surrounded by a vesicle through a single pore, forming a motionless mass at the orifice, eventually separating and either swimming directly away or undergoing a period of collective swarming in a vesicle before escaping; resting spore thick-walled, borne like the sporangium on the thallus, upon germination functioning as a prosporangium.

On the cells and gelatinous sheaths of algae and in insect exuviae.

The lack of figures in Braun's original account and the vagueness of his description have resulted in a variety of interpretations of *Rhizidium*. These have largely centered around the meaning of "two-celledness," which, together with the presence of a prolonged main rhizoidal axis, was emphasized by Braun as characteristic of *R. mycophilum*, the type species. The accepted understanding of the type species is that elaborated by Nowakowski (1876a:87; 1876b:215). He declares *R. mycophilum* to be two-celled during its whole development, one cell being the branched rhizoidal axis, the other the sporangium within which the zoospores are formed. Nowakowski's interpretation of *R. mycophilum* has been followed by most investigators, but, curiously, not his conception of *Rhizidium*. The genus has been understood by Fischer (1892:106) to include *Rhizophydioides*-like forms with subsporangial apophyses which are now placed in *Phlyctochytrium*. Earlier, Dangeard (1889b) had similarly interpreted *Rhizidium*, but included operculate as well as inoperculate species. By Zopf (1884) it was evidently at first used to include all monocentric inoperculate chytrids with tapering rhizoids. Schroeter (1885:193; 1893:79) correctly interpreted the genus and re-established *Rhizidium* in its original sense.

As understood here, *Rhizidium* includes all monocentric chytrids developing free in the medium, forming the sporangium from the enlarged body of the encysted zoospore, and having a definite taproot-like main rhizoidal axis of variable length from which arises

the great majority of rhizoids. No stress is laid upon the matter of the number of cells composing the whole plant.

KEY TO THE SPECIES OF RHIZIDIUM

- In the slime sheath of *Chaetophora* or exuviae of fresh-water insects
- Sporangium appearing tilted; the rhizoidal axis stout and elongate *R. mycophilum*, p. 276
 - Sporangium usually appearing upright; rhizoidal axis short *R. ramosum*, p. 278
- On fresh-water algae or diatoms in salt pools
- Sporangium 12–24 μ in diameter; on diatoms in salt pools *R. Braunii*, p. 279
 - Sporangium mostly 40 μ in diameter; on *Sphaerella* and *Chilomonas* *R. vorax*, p. 279

RHIZIDIUM MYCOPHILUM Braun

Monatsber. Berlin Akad., 1856: 591; Flora, 14: 599. 1856 (sensu recent).
 Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2: 88, pl. 5, figs. 6–12,
 pl. 6, figs. 1–5. 1876
 (Figure 16 E–G)

Sporangium spherical, ellipsoidal, or somewhat pyriform, borne at an angle to the prominent axis of the rhizoidal system, 25–50 μ in diameter (often up to 88 μ long by from one half to one third as broad), wall colorless, smooth, slightly thickened; main rhizoidal axis broad, 150 μ or more long, usually somewhat expanded or forming an apophysis immediately beneath the sporangium, secondary branches numerous, strongly tapering; zoospores spherical and 4–5 μ in diameter or broadly ellipsoidal and 5 μ long by 3 μ in diameter, with a single large eccentric colorless globule (rarely two) and a flagellum 30–33 μ long, emerging from the sporangium through a pore produced upon the deliquescence of a prominent papilla and forming at the orifice a motionless compact mass surrounded by evanescent slime or possibly by a vesicle, gradually falling apart and swimming away or undergoing a period of collective swarming before escaping; resting spore borne at the expanded tip of the main rhizoidal axis, spherical or ellipsoidal, 15–30 μ long, wall colorless, thick, of two layers, the inner smooth, the outer rarely smooth, generally bearing a dense feltlike covering of delicate long hairs, contents finely granular, colorless, with a single large globule, upon germination developing a small apical pore through which the contents emerge to form

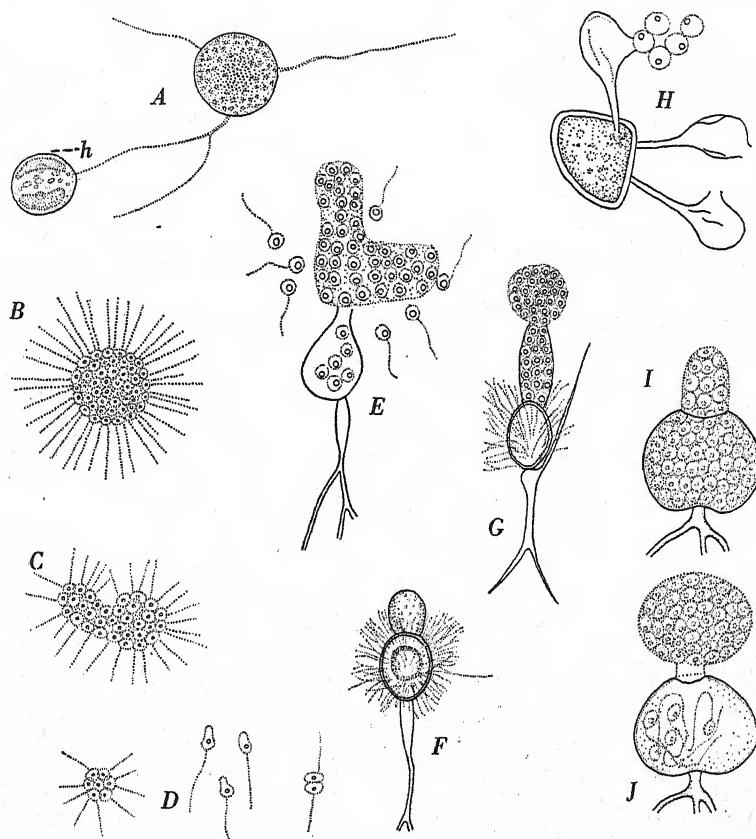


FIG. 16. Rhizidiaceae

A-D. Nowakowskia Hormotheciae Borzi ($\times 800$) parasitic on *Hormotheca*: *A*, nearly mature thallus; one branch of rhizoids is in contact with a host cell (*h*); *B*, mass of zoospores liberated upon dissolution of sporangium wall; *C-D*, stages in separation of zoospores from mass. *E-G. Rhizidium mycophilum* Braun ($\times 400$): *E*, discharging zoosporangium; the zoospores are escaping from slime mass in which they were imbedded at discharge; *F*, early stage in formation of zoosporangium at germination of resting spore; *G*, discharge of zoospores from zoosporangium formed at germination of resting spore. *H. Sporophlyctidium africanum* Sparrow ($\times 1000$) on cell of *Protoderma*; one sporangium has just discharged spores which rest near orifice; two other empty sporangia are also shown. *I-J. Rhizidium ramosum* Sparrow ($\times 750$) in insect exuviae, two stages in discharge of short-stalked sporangia.

(*A-D*, Borzi, 1885; *E-G*, Nowakowski, 1876a; *H*, Sparrow, 1938a; *I-J*, Sparrow, 1937a)

outside a long narrowly ellipsoidal or irregularly tubular zoosporangium.

In the gelatinous envelope of *Chaetophora elegans*, Braun (*loc. cit.*), Nowakowski (*loc. cit.*), GERMANY; submerged exuviae of Chironomidae (midges), Ephemeroidea (May flies), Sparrow (1937a:41, pl. 2, figs. 1-7), UNITED STATES; exuviae of Chironomidae, Sparrow (*loc. cit.*), ENGLAND.

The resting spore described by Braun for this species was brownish and rough or somewhat spiny-walled rather than covered with long hairs. Nowakowski states that the rhizoids may sometimes persist after discharge of the sporangium and a new sporangium be formed beneath the old one. This type of renewed growth was not fully described by him and needs confirmation. The inhabitant of insect exuviae differs from Nowakowski's organism chiefly in having a more spherical sporangium and an apophysis which is occasionally separated by cross walls at maturity from both the rhizoidal axis and the sporangium. There was also noted in this form a remarkable period of collective swarming of the zoospores after discharge. (See under "Nonsexual Reproduction," p. 38.)

RHIZIDIUM RAMOSUM Sparrow

Proc. Amer. Phil. Soc., 78 (1):44, pl. 2, figs. 8-13, pl. 4, fig. 1. 1937
(Figure 16 I-J, p. 277)

Sporangium globose or rarely ellipsoidal, 20-45 μ in diameter, wall slightly thickened, colorless, often bearing several irregular refractive protuberances; with a short basal main axis from which arises a system of stout branching rhizoids; zoospores ellipsoidal, 6 μ long by 4 μ in diameter, with a lateral colorless globule and a single posterior flagellum, emerging from the sporangium in a compact column after the deliquescence of a single usually terminal discharge papilla; resting spore not observed.

Saprophytic in integuments of Phryganeidae, DENMARK; Chironomidae, Ephemeroidea, UNITED STATES.

Rhizidium ramosum differs from *R. mycophilum* in possessing a very short rather than an elongated subsporangial main axis. This terminates in a profusely branched rhizoidal system. A further variation is found in the peculiar refractive nodules which occur on

some of its sporangia. Certain slight differences noted between the Danish and the American material do not, at least for the present, seem of sufficient import to separate the two as distinct species.

RHIZIDIUM BRAUNII Zopf

Nova Acta Acad. Leop.-Carol., 52 (7):349, pl. 23, figs. 1-7. 1888

Rhizophlyctis Braunii (Zopf) Fischer, Rabenhorst. Kryptogamen-Fl.,
1 (4):120. 1892.

Sporangium spherical, ellipsoidal, ovoid, or pyriform, 12-24 μ in diameter, wall thin, smooth, colorless; rhizoids well developed, several millimeters in extent, much branched, strongly polyphagous, generally arising as branches of a clavate main axis; zoospores spherical or ellipsoidal, 2.7-4 μ in diameter, with a strongly refractive globule and a flagellum, discharge not described; resting spore spherical or broadly ellipsoidal, 9-16 μ in diameter, walls thick, the outer layer gelatinous, yellowish, the inner golden brown, refractive, apparently asexually formed on a rhizoidal system like that of the sporangium, contents coarsely granular with a lateral vacuole (globule?), germination not observed.

On diatoms from a salt pool, Zopf (*loc. cit.*), GERMANY; possibly also on desmids attacked by *Rhizophyllum globosum*, Serbinow (1907: 161), FINLAND.

Minden (1915:375) has retained this fungus in *Rhizophlyctis*, but the presence of a pronounced central rhizoidal axis marks it as a species of *Rhizidium*. Serbinow's record is to be considered doubtful until further investigations indicate that the fungus inhabiting salt pools can also live in fresh water.

Rhizidium Braunii was the first species described by Fischer as representative of his new genus, *Rhizophlyctis*. Since, however, *Rhizidium* in the sense of Braun (not Fischer) was also included in *Rhizophlyctis*, the present species should have been referred to it when, subsequently, Braun's genus was reestablished in its original sense by Schroeter (1893:79).

RHIZIDIUM VORAX (Strasburger), comb. nov.

Chytridium vorax Strasburger, Jenaische Zeitschr. f. Nat., 12:564. 1878.
Rhizophlyctis vorax (Strasburger) Fischer, Rabenhorst. Kryptogamen-Fl.,
1 (4):120. 1892.

Sporangium spherical or nearly so, mostly about 40μ in diameter, wall thin, smooth, colorless, with a short lateral discharge papilla; rhizoids extensive, branched, stout, strongly polyphagous, attacking as many as from thirty to forty host cells, arising from a broad main axis attached to the base of the sporangium; zoospores spherical, 6.6μ in diameter, with a relatively large colorless basal globule, an anterior visible nucleus, and a flagellum, after discharge remaining for a time undergoing amoeboid changes of shape before rounding off and swimming away, movement swimming or amoeboid; resting spore not observed.

Parasitic on *Haematococcus lacustris* (*Sphaerella lacustris* ?), occasionally attacking resting individuals of *Chilomonas* and other swimmers, GERMANY.

Strasburger noted that the colorless zoospores were phototactic, a curious physiological adaptation to their mode of life, that is, preying on motile algae.

Though the fungus was placed by Minden, following Fischer, in *Rhizophlyctis*, Strasburger clearly states that the zoospore upon coming to rest rounds off and "... entsendet nun von einer Stelle aus, der Ciliensetzstelle so schien es mir, die sich baumartig verzweigenden Keimfaden aus."

IMPERFECTLY KNOWN SPECIES OF RHIZIDIUM

? RHIZIDIUM LIGNICOLA Lindau

Verhandl. Bot. Vereins Prov. Brandenburg, 41:xxvii, figs. 1-12. 1900

Sporangium usually more or less flattened, ellipsoidal, pyriform, or saclike, rarely spherical, sometimes with a narrow stalklike base, rounded at the top, often irregular with hornlike outgrowths, $25-75 \mu$ long by $20-25 \mu$ broad, wall thickened, colorless or somewhat brownish, resting on a vesicular apophysis formed from the body of the encysted zoospore, discharging by the deliquescence of an apical pore after the expulsion of a plug (operculum?); zoospores spherical, $2-3 \mu$ (up to 8μ in culture) in diameter, with a posterior flagellum $40-50 \mu$ long and an oil drop, discharge not observed.

Saprophytic on twigs of horse chestnut, GERMANY.

From the description given by Lindau, the fungus appears to be operculate, and the sporangium apophysate. In these characters

it more nearly resembles a species of *Nephrochytrium* except that it is epibiotic rather than endobiotic. Its development when lying free in the water is like that of *Polyphagus*. Since Lindau found the "plug" to persist at the sporangial orifice even twenty-four hours after discharge it probably should be regarded as an operculum.

EXCLUDED SPECIES OF RHIZIDIUM

* **RHIZIDIUM ALGAEOLUM** Zopf, nom. nud.¹

Nova Acta Acad. Leop.-Carol., 47:204. 1884

In manuscript, not connected with any figure or description.

On *Spirogyra*, GERMANY.

* **RHIZIDIUM EQUITANS** Zopf, nom. nud.

Pilztiere oder Schleimpilze, p. 6. Breslau, 1885

Inadequately described. Zopf later (1890:6) called this fungus "*Rhizophydiwm equitans*," also a *nomen nudum*.

* **RHIZIDIUM LEPTORHIZUM** Zopf, nom. nud.

Nova Acta Acad. Leop.-Carol., 47:231, pl. 20, fig. 5 a-c. 1884

No description in the text. Figures referred to appear to be young stages of *Rhizidiomyces apophysatus*.

* **RHIZIDIUM SPIROGYRAE** Fisch, nom. nud.

Sitzungsber. Phys.-Med. Soc. Erlangen, 16:56. 1884

A binomial (unaccompanied by a description) used in mentioning a form of *Entophysctis Vaucheriae* inhabiting *Spirogyra*.

RHIZOPHYCTIS A. FISCHER

Rabenhorst. *Kryptogamen-Fl.*, 1 (4):119. 1892 (sensu recent. Minden, Kryptogamenfl. Mark Brandenburg, 5:374. 1911 [1915])

(Figure 17, p. 284)

Thallus monocentric, eucarpic, ordinarily polyphagous, consisting of a reproductive rudiment (the body of the encysted zoospore) and

¹ Various names such as this one and combinations such as *Rhizidium olla*, *R. sphaerospermum*, and *Eurhizidium intestinum* occur in Zopf's papers. These should all be regarded as *nomina nuda*.

several branched or unbranched rhizoidal axes only the ultimate tips of which are endobiotic; sporangium inoperculate, with one or more discharge papillae; zoospores formed within the sporangium, posteriorly uniflagellate, usually with a single globule, generally discharged in a compact group imbedded in a gelatinous matrix from which they eventually escape; resting spore thick-walled, borne like the sporangium on the thallus, germination not observed.

On algae, insect integuments, and debris.

As originally described in Fischer's monograph on the Phycomycetes the genus *Rhizophlyctis* also included *Rhizidium* Braun. Schroeter (1893:79) re-established *Rhizidium* in its original sense and limited it to *Rhizidium mycophilum* Braun. *Rhizophlyctis* was retained as a genus but was not clearly separated from *Rhizidium* by him. This was later done by Minden, who emphasized the presence of a single main axis in the rhizoidal system of *Rhizidium* as contrasted with several axes, often of the same degree of development, in *Rhizophlyctis*. This morphological distinction is maintained here. Occasionally, as in *Rhizophlyctis borneensis*, the rhizoidal system may rise from a single central axis, but this is never broad and taproot-like, as in *Rhizidium*. The other extreme in rhizoidal development is to be found in *Rhizophlyctis Petersenii*, where a number of broad rhizoids emerge from the rudiment of the sporangium (Figure 17 A, p. 284). Further investigations may show these differences to be of no great significance, and the genus then should be merged with the older *Rhizidium*.

KEY TO THE SPECIES OF RHIZOPHLYCTIS

- Sporangium pyriform or bursiform, small ($12-15 \times 7-10 \mu$), zoospores few (from four to six) *R. borneensis*, p. 283
- Sporangium spherical, ovoid, ellipsoidal, clavate, or irregular and larger, zoospores numerous
 - On blue-green algae
 - Sporangium spherical or ellipsoidal, with a discharge tube, rhizoids delicate throughout; on *Calothrix* *R. Mastigotrichis*, p. 283
 - Sporangium subspherical or slightly angular, with a short

- broad apical papilla, rhizoids sometimes expanded distally;
 on *Tolypothrix* *R. Tolypotrichis*, p. 285
- On moist soil, vegetable debris, or in insect exuviae
- Sporangium mostly 22–130 μ in diameter, contents rose-red
 becoming brownish red, zoospores with a colorless globule;
 on damp soil and vegetable debris in water *R. rosea*, p. 286
- Sporangium larger, mostly 60–170 \times 40–140 μ , contents
 orange-brown, zoospores with an orange-brown globule;
 in insect exuviae and vegetable debris *R. Petersenii*, p. 287

RHIZOPHYCTIS BORNEENSIS Sparrow

Trans. Brit. Mycol. Soc., 21:150, fig. 2 f-h. 1938

Sporangium free, pyriform or bursiform, 12–15 μ long by 7–10 μ in diameter, smooth-walled, with a broad papilla; rhizoids from one to three, arising from the middle or lower part of the sporangium, generally branching in the vicinity of the host cell, polyphagous; zoospores spherical, uniflagellate, from four to six formed in a sporangium, 4 μ in diameter; resting spore not observed.

Parasitic on diatoms, coll. P. W. Richards, Sarawak.

In the shape of its sporangium this fungus closely resembles *Rhizophlyctis Mastigotrichis* (Nowak.) Fischer. It has, however, much smaller sporangia (12–15 \times 7–10 μ as compared to ones 40 μ in diameter), the rhizoids are more delicate and attenuated, not swollen distally, and a smaller number of zoospores (from four to six rather than fifty or more) are produced in each sporangium.

RHIZOPHYCTIS MASTIGOTRICHIS (Nowak.) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):121. 1892

Chytridium Mastigotrichis Nowakowski, in Cohn, Beitr. Biol. Pflanzen, 2:83, pl. 4, figs. 14–21. 1876.

Sporangium resting directly on or between the host filaments, spherical or somewhat ellipsoidal, about 40 μ in diameter, the apex prolonged into a short beak or a long tube, wall colorless, thin, smooth except in the apical region, where toothlike or small knoblike elevations may be present; rhizoids occasionally lacking, frequently from one to two, sometimes numerous, arising from the lower part of the rudiment of the sporangium, branched or unbranched, taper-

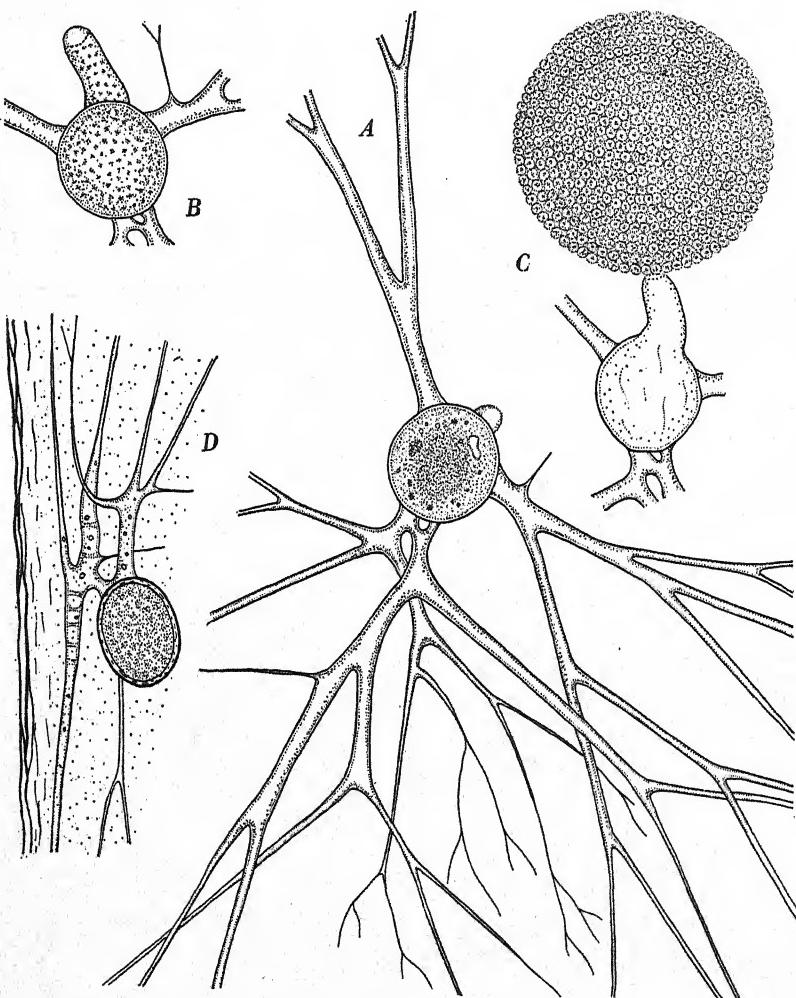


FIG. 17. *Rhizophlyctis Petersenii* Sparrow in insect exuviae

A. Mature thallus; discharge tube is beginning to form. B. Mature sporangium with discharge tube. C. Sporangium immediately after discharge; the zoospores, each with a small orange-colored oil globule, forming a motionless spherical cluster at tip of discharge tube. D. Ellipsoidal resting spore formed just beneath wall of integument. (A-C, $\times 260$; D, $\times 530$.)

(Sparrow, 1937a)

ing or the tips expanding into a somewhat spherical haustorial structure where they make contact with the host cell; zoospores large, 8 μ long by 5 μ in diameter, ovoid with a blunt rounded anterior end, possessing a large narrowly ovoid strongly refractive globule, granular near the base and with a lateral extremely refractive elongate granule, flagellum attached at the narrower end, emerging from the tip of the discharge tube and forming a spherical motionless mass surrounded by an evanescent envelope of slime, movement somewhat slow in a straight or zigzag curving line, also amoeboid; resting spore not observed.

Parasitic on *Mastigothrix (Calothrix) aeruginea*, GERMANY.

RHIZOPHYCTIS TOLYPOTRICHIS Zukal

Oesterr. botan. Zeitschr., 43:310, pl. 11, fig. 13. 1893

Sporangium resting loosely on or occasionally within the swollen sheath of the alga, subspherical, sometimes slightly angular, with a colorless wall, the inner face somewhat irregularly thickened (wavy), the outer face smooth, 22–30 μ broad, with a short broad apical papilla; rhizoids dichotomously branched or unbranched, 1.5 μ in diameter, polyphagous, the endobiotic ones often running for some distance parallel with the axis of the alga; zoospores narrowly ovoid with a broad apex, 5–6 μ long by 3–3.5 μ broad, with one flagellum and one or more colorless globules in the contents, upon discharge resting temporarily in a mass in front of the orifice before swimming away, movement swimming or hopping; resting spore (?) formed by contraction of the contents of a sporangium-like structure, spherical or somewhat angular with rounded corners, 13–17 μ in diameter, with a thick colorless smooth wall and from one to two large globules, germination not observed.

On *Tolypothrix lanata*, GERMANY.

The somewhat angular resting spores, formed in the autumn, unlike those of other species in the genus rested loosely in a sporangium-like structure.

Zukal mentions another inhabitant of *Tolypothrix* which forms a broad curving filament in the alga. He suggests tentatively that it might be *Myzocytium* but it may possibly be *Rhizosiphon* or *Resticularia*.

RHIZOPHYLYCTIS ROSEA (de Bary and Woronin) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):122. 1892

Chytridium roseum de Bary and Woronin, Berichte Verhandl. Naturforsch. Gesell. Freiburg, 3 (2):52, pl. 2, figs. 17-20. 1865.

Rhizophydiwm roseum de Bary and Woronin, loc. cit.

Sporangium spherical, ovoid, broadly clavate, or somewhat angular, 22-130 μ in diameter (occasionally only 3.3 μ), wall thick, smooth, colorless in small individuals, yellowish and minutely punctate in large ones, contents rose-red, becoming brownish red at maturity, with one or several (up to ten) broad discharge tubes filled with colorless gelatinous material; rhizoids one or more, laterally attached near the base of the sporangium or variously placed, up to 11.6 μ broad at point of origin, blunt at extremities, branched, extensive, up to 650 μ or more long, ramifying between the particles of the substrata; zoospores numerous, spherical, rose-colored, 3.3 μ in diameter, with a colorless globule and a basal dense protoplasmic spot, escaping individually or in pairs, movement hopping or amoeboid; resting spore spherical, ovoid, or irregular, with a smooth somewhat thickened wall, contents granular, with globules, olive-brown to orange-brown; germination not observed.

Forming rose-colored granulations on surface of moist soil in flower pot, de Bary and Woronin (loc. cit.), moist blotting paper, Sorauer (in Schroeter, 1885:191), GERMANY; parasitic on germinating spores of *Equisetum*, Cornu (1869b:223), FRANCE; soil, blotting paper, Couch (1939a), M. W. Ward (1939), Whiffen (in M. W. Ward, 1939), UNITED STATES; soil (coll. R. E. Coker), Cox (in Ward, 1939), GALÁPAGOS ISLANDS.

De Bary and Woronin did not consider the fungus a parasite. Cornu's observations indicated, however, that it occurred on the surface of the sand in his flats only where groups of *Equisetum* spores were found. That the latter were always arrested in their development led him to suspect that the *Rhizophlyctis* was a parasite. Schroeter (loc. cit.) describes the sporangia as being up to 250 μ in diameter.

The most complete account of the development and distribution of this species is by Miss Ward (1939). Her study indicates that it is primarily a saprophyte which can live on a variety of dead plant

tissues, cellulose, or even cellulose and corn-meal agars. Although close to *Rhizophlyctis Petersenii* in structure it differs from this species chiefly in the coloration of the contents and in having a colorless rather than an orange-brown globule in the zoospore.

RHIZOPHYLYCTIS PETERSENII Sparrow

Proc. Amer. Phil. Soc., 78(1):48, text figs. 3-4, pl. 3, figs. 1-7, pl. 4, fig. J.
1937

(Figure 17, p. 284)

Sporangia spherical or irregularly shaped, smooth-walled, the spherical specimens 50-75 μ in diameter, the irregular ones 60-170 \times 40-140 μ , contents with numerous orange-brown droplets; rhizoids arising at from one to ten places on the sporangium, stout, up to 15.6 μ in diameter near the point of origin, extensive, much branched, 500 μ or more in length; zoospores up to several hundred in a sporangium, posteriorly uniflagellate, emerging through a discharge tube up to 50 μ long by 20 μ in diameter and forming a motionless globular cluster at the orifice before dispersing, nearly spherical, 5.2 μ in diameter, with a minute orange-brown globule and several refractive granules, movement swimming or amoeboid; resting spore intercalary or rarely terminal, relatively thick-walled, spherical, ellipsoidal, or irregular, with a densely granular orange-brown content.

In submerged empty larva cases of the Chironomidae, Odonata, Sparrow (*loc. cit.*), UNITED STATES; vegetable debris, cellulose, Haskins (1939:635, figs. 1-14), CANADA.

This is the largest and most striking species of the genus. The developing thallus consists of a sporangial rudiment which, though it is generally spherical, subspherical, or ellipsoidal and free in the cavity of the exuviae, may occasionally be irregularly peltate and appressed to the inner surface of the substratum. Haskins (*loc. cit.*) has found that the fungus can be cultivated on filter paper and cellophane in pure water cultures. His organism differs from the inhabitant of exuviae in one feature. The encysted zoospore when growing on the surface of the cellophane produced a germ tube on which was ultimately formed the rudiment of the reproductive organ. If this proves to be a constant characteristic it is possible that his fungus should be removed from *Rhizophlyctis*.

IMPERFECTLY KNOWN SPECIES OF RHIZOPHYLYCTIS

? RHIZOPHYLYCTIS PALMELLACEARUM B. Schröder

'Biol. Centralbl., 18:534. 1898

Sporangia ovoid, 5-7 μ long by 3-5 μ in diameter, with a yellowish smooth wall; rhizoids profusely dichotomously branched; all other characteristics unknown.

Parasitic in cells of a palmellaceous green alga, GERMANY.

Said by Schröder to be near *Rhizidium Braunii* in its general features, but much smaller.

NOWAKOWSKIA BORZI

Bot. Centralbl., 22 (1):23. 1885

(Figure 16 A-D, p. 277)

Thallus monocentric, eucarpic, consisting of a sporangial rudiment (the body of the encysted zoospore) and from one to five rhizoids the tips of which are endobiotic; zoosporangium inoperculate, zoospores posteriorly uniflagellate, with a single globule, formed within the sporangium, liberated upon the dissolution and contraction of the sporangium wall as a flagellate compact motile group which disassociates into successively smaller groups and finally into individuals; resting spore not observed.

Parasitic on *Hormotheca*.

A monotypic genus. Differing from *Rhizophlyctis* in its method of zoospore liberation and the behavior of the freed spore mass. Some investigators have considered this behavior abnormal and have regarded the fungus as a species of *Rhizophlyctis*. From the large numbers of plants developed in Borzi's cultures, it is hardly probable that he would have selected atypical ones in characterizing his genus.

NOWAKOWSKIA HORMOTHECAE Borzi

Bot. Centralbl., 22 (1):23, pl. 1, figs. 1-10. 1885

Sporangium free in the medium, fully developed in from four to six hours, nearly spherical, 4-16 μ in diameter, with a smooth delicate colorless wall which gives a cellulose reaction, contents finely granular, multinucleate; rhizoids mostly three, rarely up to five, delicate,

tapering, emerging from any point on the surface, unbranched or occasionally branched, varying in direction and length, polyphagous; zoospores minute, elongate with a median constriction, 1μ long, flagellum posterior (?), $4-5 \mu$ long, plasma thin, homogeneous, with a basal, anterior, or lateral refractive droplet, movement of the group rolling, duration of individual motility only a few minutes; resting spore not observed.

Parasitic on germinating spores of *Hormotheca sicula*, ITALY.

The cause of an epidemic in cultures of the host.

SUBFAM. OBELIDIOIDEAE

Reproductive rudiment formed from the body of the encysted zoospore; rhizoids arising from a subsporangial apophysis; resting spore formed by conjugation of thalli by means of rhizoidal anastomosis; primarily saprophytic.

OBELIDIUM NOWAKOWSKI

Cohn, Beitrage Biol. Pflanzen, 2:86. 1876

(Figure 18 A-E, p. 292)

Mature thallus monocentric, eucarpic, consisting of a sporangial rudiment (the body of the encysted zoospore) which is differentiated into an apical solid mucro, a central thin-walled expanded sporogenous region, and a thick-walled cuplike or stalklike basal part resting on an apophysis from which radiate the main axes of the rhizoidal system; sporangium inoperculate, formed from the sporangial rudiment; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium, emerging through a lateral pore and undergoing a period of collective swarming before escaping; resting spore not observed.

Saprophytes inhabiting insect exuviae.

Obelidium in its method of development, general structural features, possession of a subsporangial apophysis, type of zoospore discharge, and habitat is very similar to the other exuviae-inhabiting fungi, *Siphonaria*, *Rhizoclostromatum*, and *Asterophlyctis*. There is little doubt but that they are all closely related forms. It is probable that when resting spores of *Obelidium* are found and their method of development followed, further similarities will be discovered.

OBELIDIUM MUCRONATUM Nowakowski

Cohn, Beitrage Biol. Pflanzen, 2:86, pl. 5, figs. 1-5. 1876

Sporangium ranging from 20-23 μ in height by 7-8 μ in diameter to 48-56 μ in height by 17-20 μ in diameter, consisting of a thick-walled cuplike or funnel-like base 4-12 μ in diameter by 4-10 μ in height, a narrowly to broadly ovoid, thin-walled mid-region, and a single solid refractive apical spine (rarely two, opposite) which is seldom more than one third of the total sporangial height; rhizoids profusely branched, extensive, radiating for 100 μ or more from their point of origin, in large specimens gradually increasing in diameter (up to 5 μ) as they approach the small subsporangial apophysis to which they are attached; zoospores spherical or slightly ellipsoidal, 2.5-3.5 μ in diameter, with a small eccentric highly refractive colorless globule and a flagellum 20 μ in length, movement hopping or amoeboid; resting spore not observed.

Saprophytic in empty submerged exuviae of Chironomidae, Nowakowski (*loc. cit.*), GERMANY; wing of submerged fly, Sorokin (1883:22, fig. 20), ASIATIC RUSSIA; Phryganeidae, H. E. Petersen (1909:412; 1910:547), DENMARK; Chironomidae, Sparrow (1938d:1, figs. 1-44), UNITED STATES.

For details of the morphology and development of this species see Sparrow (*loc. cit.*). The fungus may occasionally exhibit a *Chytridium* habit of growth, that is, the sporangium may rest on the wall of the integument (either inside or outside), the apophysis may be formed within the wall material as part of the penetration tube, and the rhizoids may extend out beyond.

Two organisms of uncertain relationships have been referred to this genus by Sparrow (1937a:48, fig. 5); both of them inhabit insect exuviae.

The first, which was tentatively called *Obelidium* (?) *mucronatum*, was found in caddis-fly integuments in Massachusetts. The sporangium was broadly fusiform, 20-33 μ long by 7-8 μ in diameter, and rested on a thick-walled cuplike base which was 3-4 μ in diameter. The apical region was thin-walled and not prolonged into a mucro, the rhizoidal system delicate, much branched, and radiating in all directions from a single point on the base of the sporangium. Discharge of the zoospores was not observed, although empty somewhat collapsed sporangia occurred.

The second, called *Obelidium hamatum*, was found in midge exuviae in New Hampshire and has been described as follows:

"Main body of the sporangium extramatrical, broadly ovoid, thick-walled, 8-9 μ in diameter by 8-12 μ in length, possessing a basal, thin-walled stalk about 4 μ in diameter by 8-12 μ in length, continuous with it, and on which are two oppositely placed, intramatrical spines; rhizoidal system intramatrical, feebly developed, branched or unbranched, emerging from the abruptly tapering tip of the intramatrical part of the stalk; zoospores ellipsoidal, 4 μ long by 2 μ in diameter, posteriorly uniciliate, uniguttulate, escaping by an opening at the base of the main body of the sporangium. Resting spores not observed."

Empty sporangia of this organism have been observed several times since, in exuviae collected in Michigan. In these instances they were entirely within the empty cavity of the exuviae. Once a single specimen was observed lying free among the tangled threads of *Mougeotia*. The new observations indicate that there is variation in the relation of the fungus to the substratum.

If further investigations seem to warrant the retention of these two fungi in *Obelidium* a modification of the genus will be necessary for their accommodation.

RHIZOCLOSMATIUM H. E. PETERSEN

Journ. de Botanique, 17:216. 1908

(Figure 18 G-I, p. 292)

Mature thallus monocentric, eucarpic, consisting of a sporangial rudiment (body of the encysted zoospore), apophysis, and delicate rhizoids; sporangium inoperculate, formed from the sporangial rudiment; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium, emerging in an evanescent vesicle to undergo a period of collective swarming before escaping, discharge pore basal, or rarely subapical or apical; resting spore borne like the sporangium on the rhizoidal system, thick-walled, sexually formed after conjugation of thalli by means of rhizoidal anastomosis, germination not observed; contributing thallus remaining small and rudimentary.

The two species thus far described are known only as saprophytes in insect exuviae.

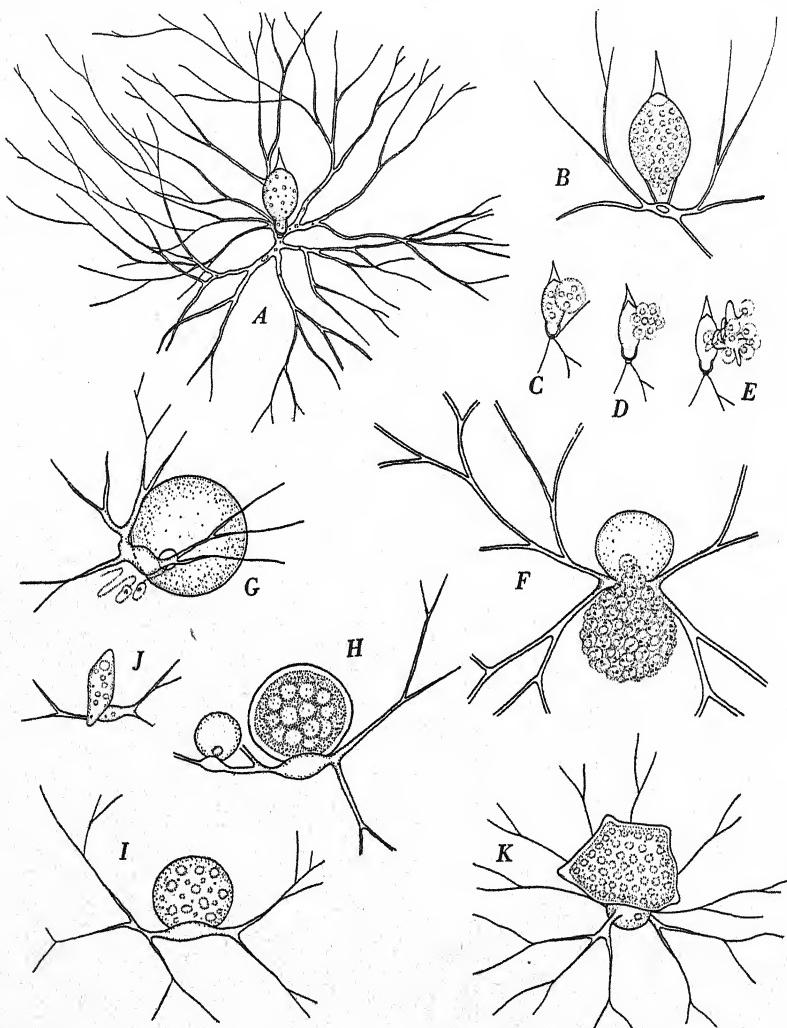


FIG. 18. Obelidioideae

A-E. Obelidium mucronatum Nowakowski (*A*, $\times 400$; *B-E*, $\times 450$): *A*, nearly complete thallus with sporangium slightly tilted; *B*, mature sporangium; *C-E*, stages in discharge of zoospores. *F. Siphonaria variabilis* H. E. Petersen ($\times 570$), discharging sporangium. *G. Rhizoclostratum aurantiacum* Sparrow ($\times 570$), empty sporangium and two zoospores. *H-I. Rhizoclostratum globosum* H. E. Petersen: *H*, small male cell attached to

KEY TO THE SPECIES OF RHIZOCLOSMATIUM

- Globule of zoospore colorless *R. globosum*, p. 293
 Globule of zoospore rusty orange *R. aurantiacum*, p. 294

RHIZOCLOSMATIUM GLOBOSUM H. E. Petersen, emend.

Journ. de Botanique, 17:216, figs. 1-2. 1903

(Fig. 18 H-I)

Sporangium spherical or subspherical, 9-22 μ in diameter (or larger), wall slightly thickened, smooth, colorless; rhizoids extensive, delicate, much branched, arising from a transverse broadly fusiform apophysis; zoospores spherical, ovoid, or ellipsoidal, 3-4 μ long by 2-3 μ in diameter, with a colorless centric or eccentric globule and a flagellum about 20 μ long, movement darting; resting spore borne like the sporangium, subspherical, 8-14 μ high by 11-20 μ in diameter, with a smooth faintly brown wall about 2 μ thick, contents with globules, germination not observed; contributing thalli from one to two, spherical, 4-6 μ in diameter, with a poorly developed rhizoidal system.

Saprophytic in empty submerged exuviae of Phryganeidae, H. E. Petersen (*loc. cit.*; 1909:415, fig. 21c; 1910:548, fig. 21c), Sparrow (1937a:38, text fig. 2 k-o, pl. 2, fig. 19), DENMARK; Chironomidae (midges), Odonata (Anisoptera) (dragonflies), Ephemerida (May flies), Phryganeidae (caddis flies), Sparrow (1937a:38, pl. 2, figs. 18, 20-24, pl. 4, figs. G-H), UNITED STATES; Chironomidae, Sparrow (1936a:418; 1937a:38), ENGLAND.

The most ubiquitous of the exuviae-inhabiting chytrids.

A form with larger sporangia and smaller zoospores, each with a rusty-red globule, has been segregated from *Rhizoclosmatum globosum* as *R. aurantiacum* Sparrow (1937a:40). Although the colorless form is most frequent it is difficult to say which one should be con-

resting spore ($\times 1000$); I, immature sporangium, showing fusiform apophysis ($\times 570$). J-K. *Asterophlyctis sarcoptoides* H. E. Petersen ($\times 570$): J, very young thallus showing irregular shape of reproductive rudiment, and apophysis from which rhizoids emerge; K, mature sporangium. All fungi figured occurred in insect exuviae.

(A-E, Sparrow, 1938d; F-K, Sparrow, 1937a)

sidered the type of *R. globosum*. Petersen's attitude (communication, 1938) is that there is no difference between the colored and colorless individuals and that ". . . the coloration in most cases is due to age or to several external factors." The original description includes both forms. In view of the observed constancy of coloration in other chytrids it is felt that the colored globule in this species is due to a genotypic factor. The name *R. globosum* has been retained, therefore, for the common colorless form.

RHIZOCLOSMATIUM AURANTIACUM Sparrow

Proc. Amer. Phil. Soc., 78(1):40, pl. 2, figs. 14-17. 1937

(Figure 18 G, p. 292)

Rhizoclosmatium globosum H. E. Petersen, pro parte, Journ. de Botanique, 17:216. 1903.

Sporangium globose, 27-38 μ in diameter, with a smooth double-contoured colorless wall; rhizoids extensive, branched, delicate, arising as stout branches from the narrower ends of a broadly fusiform transverse subsporangial apophysis; zoospores somewhat ellipsoidal, 2.5 μ long by 2 μ in diameter, with a minute rusty-orange globule and a long flagellum, escaping by a basal pore formed near the apophysis; resting spore not observed.

Saprophytic in empty submerged exuviae of Phryganeidae, H. E. Petersen (*loc. cit.*), Sparrow (*loc. cit.*), DENMARK; Odonata (Anisoptera), Chironomidae, Ephemeroidea, Sparrow (*loc. cit.*), UNITED STATES.

Distinct from *Rhizoclosmatium globosum* not only in the coloration of the globule of the zoospore but also in having larger sporangia and smaller zoospores.

ASTEROPHYLYCTIS H. E. PETERSEN

Journ. de Botanique, 17:218. 1903

(Figure 2 U, p. 46; Figure 18 J-K, p. 292)

Mature thallus monocentric, eucarpic, consisting of a somewhat angular or stellate sporangial rudiment, apophysis, and rhizoids; sporangium inoperculate, formed from the sporangial rudiment; zoospores posteriorly uniflagellate, with a single globule; resting spore borne like the sporangium on the rhizoidal system, thick-walled, stellate, sexually formed after conjugation of thalli by means

of rhizoidal anastomosis, upon germination probably functioning as a sporangium; contributing thallus remaining small.

A monotypic genus, the single species being known only in insect exuviae.

ASTEROPHYCTIS SARCOPTOIDES H. E. Petersen

Journ. de Botanique, 17:218, figs. 3-8. 1903

Sporangium irregularly stellate, colorless, with a variable number of broadly conical or acute, often thick-walled, refractive protuberances, $17-28 \mu$ broad by $18-25 \mu$ high (rarely $52 \times 33 \mu$); rhizoids originating from one or two (opposite) stout main axes extending from the spherical or subspherical ($6-11 \mu$ [rarely 13μ] in diameter) apophysis, much branched, 100μ or more in length; zoospores broadly ellipsoidal to subspherical, 5μ long by $2-3 \mu$ in diameter, with a centric or eccentric colorless globule and a long (35μ) flagellum, emerging through a basal or lateral pore $4-5 \mu$ in diameter, movement a swift darting or hopping; resting spore like the sporangium in shape but with a thicker wall, protuberances up to 9μ long, acute, nearly solid, probably functioning as a sporangium upon germination; contributing thallus somewhat ovoid, 5μ high by 4μ in diameter, thin-walled, apophysis and rhizoidal system poorly developed.

Saprophytic in empty submerged exuviae of Phryganeidae (caddis flies), Petersen (*loc. cit.*; 1909:415, fig. 21e; 1910:549, fig. 21e), Sparrow (1937a:26, text fig. 1 a-k, pl. 1, figs. 13-16, 19), DENMARK; Chironomidae (midges), Ephemera (May flies), Phryganeidae, Sparrow (*loc. cit.*, pl. 1, figs. 17-18, pl. 4, figs. D-F), May flies (MICHIGAN), UNITED STATES.

Details of the morphology and development of the species may be found in Sparrow (1937a). The occurrence of sexuality in this species has been confirmed by observations on material recently collected in Michigan. The process differs in no essential features from that found in *Siphonaria*, although the tenuity of the rhizoids and the smallness of the contributing thallus make observations extremely difficult (Fig. 2 U, p. 46). In relatively old integuments empty thick-walled resting bodies are occasionally found with a large basal pore in their walls; it is probable that zoospores were liberated through this pore at germination in the same manner as were those of the sporangia.

The form with a nearly spherical sporangium covered by small solid bipartite spines (Sparrow, 1937a: pl. 1, fig. 19) is very distinct from *Asterophlyctis sarcoptoides*, as further observations of it will no doubt reveal.

In the integuments the developing thalli strongly resemble small motionless amoebae (Fig. 18 J, p. 292).

SIPHONARIA H. E. PETERSEN

Journ. de Botanique, 17:220. 1903

(Figure 2 V-W, p. 46; Figure 18 F, p. 292)

Mature thallus monocentric, eucarpic, consisting of a sporangial rudiment (body of the encysted zoospore), apophysis, and broad, thick-walled, wide-lumened rhizoids; sporangium inoperculate, formed from the sporangial rudiment; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium, discharge pore basal; resting spore borne like the sporangium on the rhizoidal system, thick-walled, sexually formed after conjugation of thalli by means of rhizoidal anastomosis, germination not observed; contributing thallus (or thalli) remaining small and rudimentary.

A monotypic genus, known only in insect exuviae.

SIPHONARIA VARIABILIS H. E. Petersen

Journ. de Botanique, 17:220, figs. 11-17. 1903

Sporangium subglobose or broadly reniform, with a prominent basal papilla, widely variable in size, 12-39 μ in diameter by 11-36.4 μ in height (rarely 42 μ high by 38 μ in diameter), wall thin, smooth, colorless; rhizoids stout, thick-walled, wide-lumened, branched, extending from the inconspicuous apophysis formed behind the downward-tilted discharge papilla; zoospores numerous, somewhat pyriform, or ovoid, the narrower end anterior, 5 μ long by 2.5 μ in diameter, the plasma bearing a laterally placed rust-colored globule and a larger hyaline spherical body, flagellum from four to five times the length of the body, movement darting, amoeboid usually only after partial or complete retraction of the flagellum; resting spore broadly ellipsoidal or reniform, contents coarsely granular, with globules, 13-15.6 μ high by 15.6-18.2 μ in diameter, with a brown, smooth or slightly crenulated wall 2-2.5 μ thick, borne like the sporangium, the rhizoidal system, however, not so extensive, germination

not observed; contributing thallus (sometimes two) somewhat obpyriform, 7–11 μ high by 5–8 μ in diameter, rhizoidal system small.

Saprophytic in empty submerged exuviae of Phryganeidae, Petersen (*loc. cit.*; 1909:412, fig. 21 b, d; 1910:547, fig. 21 b, d), Sparrow (1937a:32, text fig. 2 a–j, pl. 1, figs. 1–12, pl. 4, figs. A–C), DENMARK; Odonata (Anisoptera) (dragonflies), Ephemerida (May flies), Sparrow (1937a:32), UNITED STATES.

Siphonaria variabilis appears to be the rarest of the chytrids inhabiting exuviae. In the Danish collections it was found in greatest numbers after the first “wave” of fungous invasion had passed, ordinarily, about a week after collection.

The early stages in the development of this species need further study. The small size of the parts renders interpretation of the details very susceptible to error. Both Petersen and Sparrow have noted the occurrence of sporangia of two size classes. This suggests the possibility that sexual differentiation of the zoospores may be present.

SUBFAM. POLYPHAGOIDEAE

Reproductive rudiment formed as an outgrowth from the body of the encysted zoospore; resting spore sexually produced by conjugation of directly adnate thalli or thalli joined by a conjugation tube; parasitic on fresh-water algae.

POLYPHAGUS NOWAKOWSKI

Cohn, Beitr. Biol. Pflanzen, 2:203. 1876

(Figure 2 Z–Z', p. 46; Figure 19 F–I, p. 302)

Thallus generally lying free in the medium, monocentric, eucarpic, consisting of an expanded central part, the rudiment of the prosporangium, from which arise from two to three or more rhizoidal axes, the rhizoids profusely developed, much branched, strongly polyphagous, only the tips endobiotic; sporangium inoperculate, formed as an outgrowth from the prosporangium, from which it is cut off at maturity by a cross wall; zoospores posteriorly uniflagellate, with a single globule, completely formed in the sporangium, liberated through a pore produced in the wall of the sporangium; resting spore thick-walled, with a large globule, produced by the fusion of two

anisogamous aplanogametes in the distal part of a conjugation tube formed generally by the smaller of two thallus-like gametangia, upon germination functioning as a prosporangium.

The species have thus far been found only as parasites of *Euglena*, *Chlamydomonas*, and *Tribonema*.

Because of the early researches of Nowakowski (1876b; 1878) supplemented by later accounts of the morphology and cytology by Dangeard (1886a; 1900-1901c), Wager (1899a; 1913), and Scherffel (1925b), *Polyphagus* has become one of the best known of the chytrids. The strongly polyphagous thallus of *P. Euglenae* is ordinarily profusely developed, and both nonsexual and sexual reproductive organs are readily formed. Since the resting spore germinates after a relatively brief period of quiescence the whole life cycle can be easily followed in a short time, a situation of uncommon occurrence among the chytrids.

The most ubiquitous species is *Polyphagus Euglenae*. *P. parasiticus* has also been reported in Europe by Scherffel (*loc. cit.*), who has given an extensive account of its morphology and life history, and in the United States by Sparrow (1939a). It occurred as a parasite of *Tribonema bombycinum*. Raciborski's *P. Nowakowskii*, on *Chlamydomonas* in Java, has been recorded only by him.

It is difficult to give clear-cut lines of demarcation between the species. Raciborski's fungus appears to differ from the others chiefly in forming smaller, colorless zoospores.

KEY TO THE SPECIES OF POLYPHAGUS

Parasitic on *Euglena* and *Chlamydomonas*

- Zoospores cylindrical, with broad rounded ends, $6-13 \times 3-5 \mu$, globule golden *P. Euglenae*, p. 298
- Zoospores spherical, 4μ in diameter, globule colorless *P. Nowakowskii*, p. 300

Parasitic on filaments of *Tribonema*, zoospores as in *P. Euglenae*

P. parasiticus, p. 301

POLYPHAGUS EUGLENAE Nowakowski

Cohn, Beitr. Biol. Pflanzen, 2:203, pl. 8, figs. 1-12, pl. 9, figs. 1, 16. 1876
(Figure 19 F-G, p. 302)

Prosporangium free in the medium, rarely sessile, usually borne on a more or less elongate broad rhizoid, spherical, ovoid, ellipsoidal,

clavate, or somewhat irregular, variable in size, 10–37 μ in diameter, wall thin or slightly thickened, smooth, colorless; rhizoidal system profusely developed, much branched, arising at from two to six places on the rudiment of the prosporangium, the axis first formed generally stouter than the others, its tip endobiotic and unbranched; sporangium of variable shape, predominantly irregularly tubular and gibbose, with a slightly broader base, sometimes ovoid, ellipsoidal, or short-cylindrical, wall smooth, colorless, thin or occasionally somewhat thickened, up to 275 μ in length (small examples 30 μ or less) by 8–30 μ or more in diameter; zoospores cylindrical, with broad rounded ends, variable in size, largest 13 μ long by 5 μ wide, smallest 6 \times 3 μ , contents vacuolate, with a basal pale-golden oil globule and a long flagellum, emerging individually through an apical pore or, rarely, released upon the deliquescence of the whole upper part of the sporangium, in any case generally swimming directly away, although occasionally remaining in a vibrating mass at the orifice before dispersing, positively phototactic; resting spore spherical, ovoid, ellipsoidal, or somewhat irregular, with a thick double wall, the exospore brownish and minutely spiny or bullate, the endospore smooth and colorless, predominantly formed in the distal part of a more or less elongate clavate conjugation tube, upon germination functioning as a prosporangium.

On *Euglena sanguinia*, Gross (1851), *Euglena* sp., Bail (1855:678), *E. viridis*, Nowakowski (*loc. cit.*; 1878:181), *Euglena* sp., Fisch (1884a), Minden (1915:382, fig. 28f [p. 364]), GERMANY; *Euglena*, Entz, Sr. (1873:1, pl. 1, figs. 12–17, pl. 2, figs. 6–8), HUNGARY; *Euglena viridis*, Blytt (1882:29), NORWAY; *Euglena* sp., Dangeard (1886a:303, pl. 13, figs. 31–35; 1900–1901c:213, figs. 2–3, pls. 6–7), FRANCE; *Euglena* sp., de Wildeman (1890:27), BELGIUM; encysted *Chlamydomonas Reinhardi*, Serbinow (1907:163), RUSSIA; *Euglena* sp., H. E. Petersen (1909:410; 1910:544), Sparrow (1936a:453), DENMARK; *Euglena viridis*, Wager (1913:173, pls. 16–19), ENGLAND; cysts of *Euglena viridis* and *Chlamydomonas* sp., Valkanov (1931a: 365), BULGARIA; *Euglena viridis*, Graff (1928:165), UNITED STATES.

In his account of *Polyphagus Euglenae* Nowakowski asserted that the smooth-walled spores are formed after the contents of the female gametangium have emerged and become fertilized by the male. This has never been confirmed by subsequent investigations.

Encysted prosporangia have been noted in *Polyphagus Euglenae*

by Dangeard and Wager. These are uninucleate and germinate to form a small sporangium. Sporangia of two size classes have been noted, as has also a relatively wide variation in the size of the zoospores. The possibility of the occurrence of sexual differentiation of the zoospores, as suggested by Kniep (1928), should not be overlooked in future investigations of this species.

The cytology of the species is well known from the researches of Dangeard and Wager (see "Cytology," p. 57).

P. EUGLENAE var. MINOR Nowakowski, Akad. umiejetności Krakowie. Wydział mat.-przyrōd., Pamietnik, 4:174, pl. 10, figs. 97-100. 1878. (Figure 2 Z-Z', p. 46.)

This variety resembles *Polyphagus Euglena*, but the resting spore is smooth-walled and more ovoid, or ellipsoid.

On *Euglena*, Dangeard (*loc. cit.*), FRANCE; *Euglena*, Nowakowski (*loc. cit.*), Minden (*loc. cit.*), GERMANY; *Euglena*, Constantineanu (1901:383), RUMANIA; *Euglena* sp., Wager (*loc. cit.*), Sparrow (1936a: 453, pl. 14, figs. 21-22; 1935a: fig. 2 h-i), ENGLAND; *Chlamydomonas*, Skvortzow (1927:206), MANCHURIA.

In his 1876 paper Nowakowski called attention to the occurrence in *Polyphagus Euglena* of ornamented and smooth-walled races. Owing to the lack of data on the nature of the resting-spore wall in successive generations, however, these were not separated as distinct species. Wager contends that the two types of wall are produced by the same species under varying conditions of nutriment. It seems more probable that two species are involved. This has been intimated by Nowakowski in his separation of the smooth-walled form as var. *minor*.

POLYPHAGUS NOWAKOWSKII Raciborski

Parasitische Algen und Pilze Java's, p. 6. Batavia, 1900

Prosporangium spherical, thin-walled, 9-16 μ in diameter, with several long branched delicate rhizoids the tips of which enter the host cells; sporangium variable in shape, unsymmetrical, mostly ovoid, with a broad base, larger than the prosporangium; zoospores spherical, 4 μ in diameter, with a colorless globule and a long flagellum; resting spore spherical, ovoid, elongate, or narrowly biscuit-shaped, 12-22 μ long by 8-12 μ broad, with a smooth yellowish thick wall, germination not observed.

Parasitic on *Chlamydomonas plurialis*, JAVA, DUTCH EAST INDIES.

POLYPHAGUS PARASITICUS Nowakowski

Akad. umiej. Krakowie. Wydział mat.-przyród., Pamietnik, 4:174,
pl. 10, figs. 101-107. 1878

(Figure 19 H-J, p. 302)

Prosporangium lying free between the filaments of the host, pyriform, clavate, or irregularly broadly fusiform, terminal or more often intercalary between two opposite main rhizoidal axes, from which, as well as from the body, arise more delicate branched rhizoids; sporangium generally formed as a lateral outgrowth from the prosporangium, ovoid, 16μ long by 14μ broad, wall thin, colorless; zoospores few, spherical, $6-8 \mu$ in diameter, with a large (4μ) colorless basal globule and a long flagellum, escaping upon the gelatinization of the upper half of the sporangium wall; resting spore formed from the tip of the laterally or apically applied conjugation tube, spherical, $9-18 \mu$ (mostly $12-14 \mu$) in diameter, with a thick brownish wall covered with short conical spines, contents bearing a large ($7-14 \mu$ in diameter) colorless globule, upon germination functioning as a prosporangium.

Parasitic in *Tribonema bombycina*, Nowakowski (*loc. cit.*), GERMANY (?); Scherffel (1902a; 1904; 1925b:2, pl. 1, figs. 1-10), HUNGARY; Sparrow, UNITED STATES (MICHIGAN).

Scherffel (1925b) has given a complete account of this little-known species. In Michigan it is found in early spring among filaments of *Tribonema*.

SPOROPHYLYCTIS SERBINOW

Scripta Bot. Horti Univ. Imper. Petro., 24:163. 1907

(Figure 19 C-E, p. 302)

Thallus monocentric, eucarpic, consisting of a reproductive rudiment (the body of the encysted aplanospore) and a tapering main rhizoidal axis from which arise numerous secondary branches, tips of the ultimate branches endobiotic; prosporangium developed from the body of the aplanospore; aplanospores formed in an inoperculate thin-walled sporangium produced laterally on the prosporangium, liberated upon the rupturing of the sporangium wall; resting spore thick-walled, formed by the receptive thallus after conjugation of two like-sized, similar thalli, the receptive thallus in the process forming a tube which penetrates the contributing thallus and through

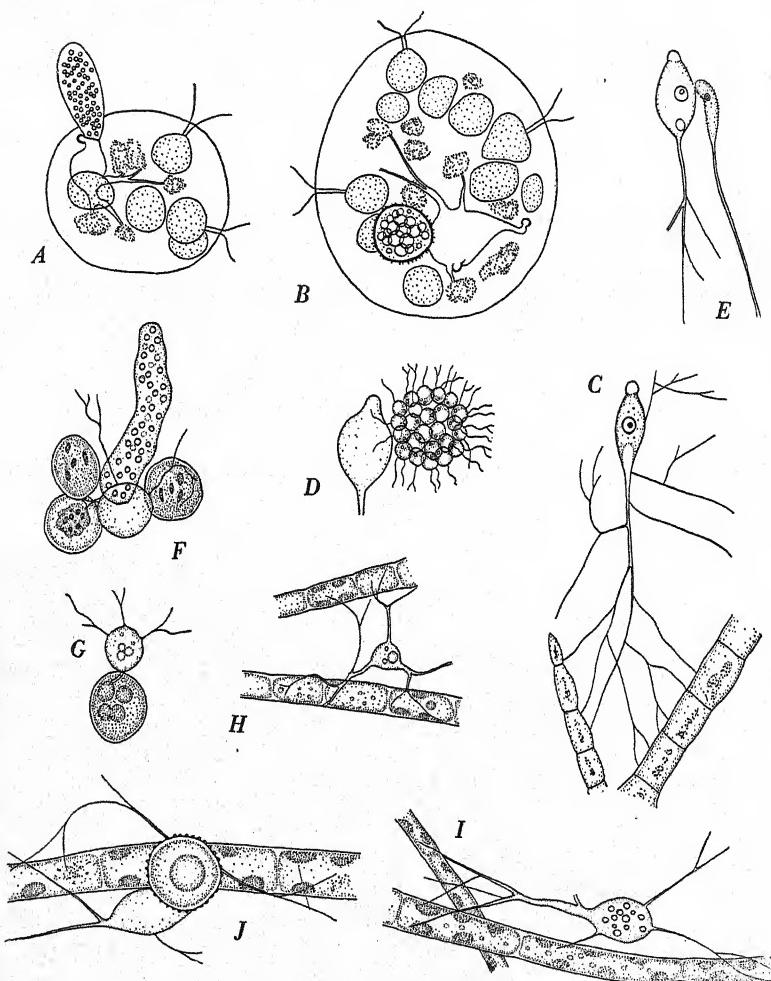


FIG. 19. Polyphagoideae

A-B. Endocoenobium Eudorinae Ingold ($\times 325$) on colony of *Eudorina*: *A*, thallus with mature zoosporangium; thick-walled cyst of zoospore is at base of sporangium; *B*, mature spiny resting spore formed after fusion of two thalli. *C-E. Sporophlyctis rostrata* Serbinow on *Draparnaldia*: *C*, uninucleate thallus with rhizoids penetrating alga; *D*, group of aplanospores which have germinated after discharge from sporangium; *E*, male (smooth) and female (spiny) gametangia. *F-G. Polyphagus Euglenae* Nowakowski ($\times 400$): *F*, small mature sporangium produced from prosporangium resting

which most of the contents of the latter are discharged, germination not observed.

A monotypic genus; so far as is known parasitic only on the freshwater green alga *Draparnaldia*, an inhabitant of cool, clear, running water.

SPOROPHLYCTIS ROSTRATA Serbinow

Scripta Bot. Horti Univ. Imper. Petro., 24:163, pl. 1, figs. 13-16, pl. 2, figs. 17-35. 1907

Prosporangium ovoid, with a prominent apiculus, 30-39.5 μ long by 9-12.7 μ in diameter, wall thin, smooth, colorless, sporangium spherical or somewhat ellipsoidal, thin-walled, 23.7-31.6 μ in diameter ("20.5-26.8 μ \times 23.7-35.5 μ " [Serbinow, 1907]); rhizoids much branched, arising from the main axis or also occasionally from the body of the sporangium; aplanospores spherical, with a small eccentric colorless globule, germinating in the sporangium or upon the rupturing of its wall, free in the medium; resting spore ovoid, acuminate, 31.5 μ long by 23.5 μ wide, thick-walled, pale brown, the outer surface covered with minute spines, contents with a single globule, germination not observed; contributing thallus ovoid, smooth-walled.

Parasitic on *Draparnaldia glomerata*, Serbinow (*loc. cit.*), RUSSIA; *Draparnaldia plumosa*, Graff (1928:166), UNITED STATES.

The immature thallus on *Draparnaldia* from Denmark figured by Petersen (1909:410, fig. 20b; 1910:fig. 20b) and doubtfully assigned to *Sporophlyctis rostrata* is very probably this species.

ENDOCOENOBIUM INGOLD

New Phytologist, 39:97. 1940

(Figure 19 A-B)

"The thallus is microscopic, living within the coenobium of members of the Volvocales. From the sac-like thallus rhizoidal outgrowths, branched or unbranched, make contact with the host cells. The

between three parasitized cysts of *Euglena*; G, very young thallus resting directly on *Euglena*. H-J. *Polyphagus parasiticus* Nowakowski ($\times 900$) on *Tribonema*: H-I, young thalli lying between filaments of host; J, mature resting spore.

(A-B, Ingold, 1940; C-E, Serbinow, 1907)

thallus is not produced by the direct enlargement of the encysted zoospore, but by the enlargement of an outgrowth from it. The encysted zoospore persists on the surface of the host coenobium. The zoosporangium is elongated, and cut off from the thallus by a cross wall. Dehiscence is by an apical tear. The zoospores are uni-ciliate. The thick-walled resting spores are produced following a sexual process. In this process two thalli, which have developed in the same coenobium, fuse, and from the fusion-cell a warted zygospore is budded off" (Ingold, *loc. cit.*).

A monotypic genus on *Eudorina elegans*, England.

ENDOCOENOBIUM EUDORINAE Ingold

New Phytologist, 39:97, figs. 1-4, pl. 2. 1940

Characters of the genus.

The curious type of sexual reproduction found in this most interesting fungus warrants further investigation.

CLADOCHYTRIACEAE

Thallus intra- or extramatrical, or both, eucarpic, usually strongly polycentric, the vegetative system extensive, much branched, tubular, rhizoidal, septate or nonseptate, often with irregular swellings and septate turbinate cells; sporangia inoperculate, terminal or intercalary, zoospores posteriorly uniflagellate (the flagellum apparently lacking in one genus), with a single globule; resting spores thick-walled, apparently asexually formed, borne like the sporangia on the rhizoidal system, upon germination functioning as a zoosporangium.

Primarily saprophytic in decaying vegetable debris and parasitic in the eggs of microscopic animals and in fresh-water algae. One genus parasitic in marine algae.

Because of the remarkable alternation of an epibiotic monocentric phase with an independent endobiotic strongly polycentric one, the genus *Physoderma*, usually included here, is maintained distinct from the Cladochytriaceae, and might well be placed in a family of its own—the Physodermataceae (see under "*Cladochytrium*," p. 306).

KEY TO THE SUBFAMILIES AND GENERA OF THE
CLADOCHYTRIACEAE¹

- Vegetative system predominantly rhizoidal and nonseptate except for the turbinate cells Subfamily CLADOCHYTRIOIDEAE, p. 305
- Zoospores flagellate, sporangia internally proliferous
- Sporangia and rhizoids predominantly endobiotic, the sporangia terminal or intercalary, often apophysate, with a discharge tube; zoospores at discharge forming a temporary motionless group CLADOCHYTRIUM, p. 305
- Sporangia and rhizoids predominantly extramatrical, sporangia without a discharge tube, borne at the tips of the rhizoids; zoospores at discharge swarming for a time in a vesicle at the orifice PHYSOCLADIA, p. 315
- Zoospores nonflagellate, strongly amoeboid, sporangia not proliferating AMOEBOCHYTRIUM, p. 317
- Vegetative system predominantly tubular and septate, with or without secondary rhizoidal axes. Subfamily CATENARIOIDEAE, p. 317
- Vegetative system endobiotic with secondary rhizoidal axes, the endobiotic sporangia separated by sterile septate isthmuses
- CATENARIA, p. 318
- Vegetative system extramatrical or endobiotic without secondary rhizoidal axes, tubular and septate throughout, sporangia extramatrical COENOMYCES, p. 321

SUBFAM. CLADOCHYTRIOIDEAE

Vegetative system predominantly rhizoidal and nonseptate except for the turbinate cells.

CLADOCHYTRIUM NOWAKOWSKI, pro parte

Cohn, Beitr. Biol. Pflanzen, 2:92. 1876 (sensu recent. Schroeter, in Engler and Prantl, Natürlichen Pflanzenfam., 1 [1]:81. 1893)

(Figure 20I, p. 314)

Thallus predominantly endobiotic, polycentric, eucarpic, consisting of an extensive much-branched rhizoidal system on which are formed irregular swellings, septate turbinate cells, and the rudiments of the sporangia and resting spores; sporangia inoperculate, inter-

¹ See also *Polychytrium* Ajello, *Mycologia*, 34:442. 1942.

calary or terminal on short lateral branches, with a discharge tube, often proliferating; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium, discharged through a pore at the tip of the discharge tube; resting spores apparently asexually formed, borne like the sporangia on the thallus, with a thickened smooth or spiny wall, upon germination forming zoospores which escape through a discharge tube.

Species of the genus are primarily inhabitants of decaying plant tissues such as those of *Acorus*, grass stems, *Elodea*, and the like. They have also been found in the gelatinous envelope of *Chaetophora* and in plants of *Spirogyra*, *Coleochaete*, and so forth. One species (*Cladochytrium replicatum*) has been cultivated on artificial media.

The genus as originally defined by Nowakowski included both inoperculate and operculate forms. The latter were rightly segregated from *Cladochytrium* by Schroeter (*loc. cit.*) and placed in a new genus, *Nowakowskella*. From Nowakowski's description, *C. tenue* can be considered typical of his genus. Here the sporangia are endobiotic, thin-walled, and discharge their zoospores through a tube to the outside of the substratum. Resting spores have not thus far been found in this species, but in the closely related *C. replicatum*, where they have been observed, they are borne on the thallus in the same fashion as are the sporangia (Sparrow, 1933c: 524, pl. 49, fig. 3; Karling, 1935:449, figs. 21-29). At germination they form a discharge tube through which zoospores emerge.¹

Unfortunately, de Bary (1884:178) placed in Nowakowski's genus a series of parasites of flowering plants which had a vegetative system like that of *Cladochytrium tenue* but which bore only thick-walled, generally somewhat ellipsoidal, resting spores, usually flattened on one face. The inclusion of this series of chytrids—all referable to *Physoderma* in the modern sense—was formalized by Fischer (1892: 131), who divided *Cladochytrium* into three subgenera: (1) *Cladosporangium*, including *C. tenue*, *C. polystomum*, and *C. elegans* (*Nowakowskella*), in which the endobiotic sporangium discharged by a tube; (2) *Urophlyctis*, in which the sporangium was epibiotic and sessile, the resting spores endobiotic; and (3) *Physoderma*, in which

¹ See, however, Karling's recent paper (*Torreya*, 41:105. 1942), where they are described as functioning as prosporangia.

the zoosporangia were lacking and only endobiotic thick-walled resting spores formed on an evanescent rhizoidal system. This arrangement differed from the earlier one of Schroeter (1885) chiefly in reducing to subgenera of *Cladochytrium* the genus *Physoderma* of Wallroth (1833) and Schroeter's genus *Urophlyctis*. These two genera were distinguished from each other by both Schroeter and Fischer on the presence or absence of ephemeral epibiotic sporangia. This remarkable stage was apparently originally observed by Schroeter (1883) in *P. (Urophlyctis) pulposa*. The zoospores from these sporangia at first formed on the young host plants new epibiotic sporangia with a short bushy endobiotic rhizoidal system. Later the zoospores formed germ tubes which penetrated the host and produced resting spores endobiotically, each of which, Schroeter asserted, was formed after some sort of copulation. The existence of the epibiotic stage in "*Cladochytrium*"-like fungi was confirmed by Büsgen (1887) in *Cladochytrium (Physoderma) Butomi* and in later years by Clinton (1902) in *P. maculare* and by Sparrow (1934a) in *P. Menyanthis* and *P. Zeae-maydis*. The discovery of the epibiotic stage in *P. maculare* by Clinton was of particular interest. De Bary (1864) had examined Wallroth's original specimens and found the typical ovoid flattened resting spores. Clinton's material differed in no essential respects from Wallroth's, and there seems little question of the identity of the two forms. The significance of Clinton's findings are evident when we appreciate that his fungus, an unquestioned species of *Physoderma*, was found to have the epibiotic stage characteristic of Schroeter's genus *Urophlyctis*. The other feature said to distinguish Schroeter's *Urophlyctis*, namely, the conjugation process previous to the resting-spore formation, although upheld by Magnus (1897, 1902a, 1902b) has not been borne out by other researches (see Vuillemin, 1896; Bally, 1911; Maire and Tison, 1911a; Line, 1921; and particularly Jones and Drechsler, 1921). Magnus also attempted to distinguish *Urophlyctis* from *Physoderma* by the reactions of the host plant to the fungus. He assigned to *Urophlyctis* forms producing a pronounced thickening of the host wall and general hypertrophy of the infected region, and to *Physoderma* those which had little effect on the host tissue. This difference has been emphasized by Minden (1915) in distinguishing the two. Jones and Drechsler, however, point out "... a distinction on such grounds would make the classification of parasitic forms contingent in too large a measure

on reactions of the host plant to be admissible in a taxonomic sense." On morphological grounds, therefore, there seems no justification for maintaining *Urophlyctis* apart from *Physoderma*.

There are, however, very definite bases for distinction between *Cladophytrium* and *Physoderma*. This distinction is not founded on the absence of resting spores in *Cladophytrium* or on their presence, structure, and type of germination (by a germ tube) (Karling 1931b: 542; 1934b:390), but primarily on the differences in thallus organization. In *Cladophytrium* the zoosporangia are formed endobiotically on an endobiotic polycentric thallus. On the same thallus (see Karling, 1937b:pl. 6) are developed the hyaline, relatively thin-walled resting spores. Each of the latter produces upon germination a discharge tube and functions as a sporangium.¹ In *Physoderma* the extensive polycentric endobiotic thallus has never been observed to give rise to any type of reproductive organ save the thick-walled, flattened, elliptical, usually colored resting spores. Each of these upon germination cracks open and produces a sporangium as a sac-like extrusion. The zoospores from this sporangium come to rest on the surface of the host cell and form epibiotic sporangia, each of which has a bushy monophagous rhizoidal system. This phase is definitely epibiotic, monocentric, and monophagous as contrasted with the strongly polycentric and polyphagous phase within the host in which the resting spores are formed. What connection exists between these two thalli is not at present known. It seems logical to suppose that the "sporangia" are in reality gametangia, the "zoospores," gametes, and the endobiotic phase diploid in nature (Sparrow, 1940a). Reduction division would then occur upon the germination of the resting spore. There is, however, no evidence as yet to confirm this hypothesis.

It can be seen that, save for a superficial resemblance in thallus structure, *Cladophytrium* and *Physoderma* are distinct groups of fungi and cannot be regarded as generically synonymous.

KEY TO THE SPECIES OF CLADOPHYTRIUM²

- | | |
|--|-------------------------------|
| Globule of zoospores colorless | <i>C. tenue</i> , p. 309 |
| Globule of zoospores orange | <i>C. replicatum</i> , p. 310 |

¹ See p. 306 n.

² See also *Cladophytrium hyalinum* Berdan, Amer. J. Bot., 28:425. 1941, and *C. crassum* Hillegas, Mycologia, 33:618. 1941.

CLADOCHYTRIUM TENUE Nowakowski

Cohn, Beitr. Biol. Pflanzen, 2:92, pl. 6, figs. 6-13. 1876
(Figure 20 I, p. 314)

Sporangia intra- or extramatrical, formed from a swelling of the rhizoid or by enlargement of a segment of a septate turbinate cell, when the sterile segment either remains at the base as an empty appendage or eventually becomes a sporangium, spherical or somewhat pyriform, up to 66μ in diameter (averaging about 18μ), with a more or less prolonged regular or irregular rather stout discharge tube (rarely several) the tip of which is either extramatrical or penetrates a neighboring cell, wall smooth, colorless, proliferating, the secondary sporangia smaller; rhizoidal system extensive, branching, the rhizoids $1-2 \mu$ in diameter, with spindle-shaped or spherical swellings which are often transversely septate and divided into two equal parts (occasionally three); zoospores spherical, 5μ in diameter, with a colorless eccentric globule and a posterior flagellum, emerging upon the deliquescence of the tip of the discharge tube and forming a temporary motionless mass imbedded in "slime," movement amoeboid or swimming; resting spores not observed.

In decaying tissues of *Acorus Calamus*, *Iris pseudoacorus*, *Glyceria spectabilis*, Nowakowski (*loc. cit.*), GERMANY; *Hippuris vulgaris*, de Wildeman (1895b:91, pl. 3, figs. 14-23), FRANCE; leaves of "Massette," Constantineanu (1901:385), RUMANIA; *Acorus Calamus*, Sparrow, UNITED STATES (MICHIGAN).

The zoospore at germination produces one or two delicate filaments, which after a few days become elongate and irregularly branched. Spindle-shaped swellings soon appear, and the sporangia are later formed from some of these.

De Wildeman's record is doubtful, since no zoospore discharge was observed. The same might be said for the reported occurrence in Rumania. In the material from Michigan opportunity was afforded to compare the species with *Cladochytrium replicatum*, with which it was growing. Aside from the absence of coloration in the zoospore globules, *C. tenue* also differed from *C. replicatum* in the infrequency of formation of turbinate cells, in the pronounced tendency of the rhizoids suddenly to expand irregularly along their length, and in the formation of a broader more irregular discharge tube. A less noticeable but constant difference between the two was the

disposition of the globules of the zoospores in the sporangium. In *C. replicatum* these were generally clustered in the center, whereas in *C. tenue* they were more regularly dispersed throughout. The Michigan material differed from Nowakowski's only in having a slightly smaller oil globule in the zoospore.

CLADOCHYTRIUM REPLICATUM Karling

Amer. J. Bot., 18:538, pl. 42-44. 1931

Cladochytrium Nowakowskii Sparrow, Amer. J. Bot., 18:619, pl. 45, figs. H-N. 1931.

Entophyscia aurantiaca Scherffel, in Domján, Folia cryptogam., 2:26, pl. 1, figs. 50-51, 57-59, 72-73, 75. 1936.

Sporangia generally terminal on short lateral branches, predominantly spherical, ovoid, or pyriform and free in the cell of the substratum, or sometimes filling it and becoming irregular, symmetrical sporangia 8-18 μ in diameter, with a single narrowly cylindrical discharge tube of variable length (occasionally several), wall thin, smooth, colorless, proliferating; rhizoidal system delicate, much branched, extensive, bearing septate turbinate cells at frequent intervals; zoospores variable in number, spherical, 4-7.3 μ in diameter, with a cadmium-orange or golden-brown globule and a long flagellum, emerging through the tip of the discharge tube and forming a temporary motionless group at the orifice before swimming away, movement swimming or amoeboid; resting spores borne like the sporangia on the thallus, predominantly spherical, 9-21 μ in diameter, with a thickened spiny or smooth colorless wall and a large cadmium-orange or golden-brown globule in the contents, upon germination producing a discharge tube and functioning as a zoosporangium.¹

Saprophytic in a wide variety of vegetable materials and artificial media, Karling (1931b; 1935), parasitic in *Spirogyra crassa*, *Oedogonium spp.*, *Coleochaete sp.*, cultivated on maize-meal agar, Sparrow (*loc. cit.*), saprophytic in *Anacharis canadensis*, decaying grass culms, Sparrow (1933c:524, pl. 49, fig. 3), artificial media, Couch (1939a), UNITED STATES; saprophytic in *Anacharis canadensis*, grass, Sparrow (1936a:453), ENGLAND; *Typha* leaves, Scherffel (in Domján, 1936), HUNGARY.

This is one of the most ubiquitous species of the chytrids, and submerged decayed bits of the softer parts of phanerogams which

¹ See, however, Karling, as cited on p. 306 n.

do not contain it are rarely found. The species is readily distinguished from the less common *Cladochytrium tenue* by the brilliantly colored globules of the spores. This coloration makes its appearance early in the development of the sporangium. Other differences between the two have already been mentioned (see *C. tenue*).

It remains a question whether or not *Cladochytrium Nowakowskii* is identical with the present species. The fungus was found in a well-balanced algal culture and was observed to infect three genera of the Chlorophyceae. Observations by Karling and later ones by Sparrow on what appears morphologically to be the same species indicate that it is primarily saprophytic.

The fungus was grown on maize-meal agar by Sparrow (1931c), but could not be freed from bacterial contamination. It was later cultivated by Karling (1935) and Couch (1939a), not only on maize-meal agar but also on prune, malt, potato-dextrose, and mannite-soil agars. Karling found that sporangia were formed only in liquid media. Of the agars used, maize meal and mannite soil were most favorable.

A cytological investigation of the species has been made by Karling (1937b) (see under "Cytology," p. 59).

IMPERFECTLY KNOWN SPECIES OF CLADOCYTRIUM¹

? CLADOCYTRIUM CORNUTUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 20:59, pl. 3, figs. 1-22. 1896

Sporangia formed extramatrically, subspherical or reniform, apophysate, not separated from the vegetative system by a cross wall, with a crown of from three to seven coarse plain teeth; rhizoidal system endobiotic, branched, extensive, with fusiform swellings; zoospores spherical, uniflagellate, with a small refractive eccentric globule, probably escaping through a pore formed within the apical collarette of teeth; resting spores not observed.

In rotting plant tissues, in company with *Cladochytrium tenue*, FRANCE.

Although the species is obviously distinct from other members of *Cladochytrium* by reason of the ornamentation of the sporangium, some features of it are puzzling. De Wildeman has shown in Figure

¹ For a discussion of certain shell-boring organisms supposedly belonging to this genus see pp. 313, 315.

14 an empty sporangium within which are three empty saclike structures. These he thinks belong to a parasitic organism. Over half the figures of mature sporangia shown have "vacuoles" within them which in some cases approximate in size and shape the empty sporangia of the parasitic organism. Earlier monographers have doubted the validity of the species. This is not questioned here, yet the possibility that the concept is based on parasitized and hypertrophied specimens of *Phlyctochytrium planicorne*—found in the same habitat—cannot be entirely excluded.

? CLADOCYTRIUM IRREGULARE de Wildeman

Ann. Soc. Belge Micro. (Mém.), 19:91, pl. 3, figs. 1-13. 1895

A fungus parasitic in aquatic grasses with irregular tubular sporangia which resemble those of *Mitocytridium* and which are 200-235 (?) μ long by 15-40 μ wide and borne on a branched rhizoidal system has been called a species of this genus by de Wildeman (*loc. cit.*). No zoospores were observed, and its affinities are in doubt.

? CLADOCYTRIUM POLYSTOMUM Zopf

Nova Acta Acad. Leop.-Carol., 47:234, pl. 21, figs. 1-11. 1884

Sporangia spherical or fusiform, intercalary, originating as spindle-shaped enlargements on the vegetative system, forming from one to six long irregular discharge tubes; vegetative system extensive, branched, slender, rhizoidal; zoospores spherical with a brownish-orange oil globule; resting spores not observed.

In *Triaena*, GERMANY.

No description of the fungus occurs in Zopf's text, and a formal description was first given by Fischer (1892:135).

An estimation of the sizes of the parts, arrived at by using as a measure the zoospore of *Rhizophyridium carpophilum*, which is described as 4-5 μ in diameter and is drawn to the same magnification, indicates that the sporangia of *Cladocytrium polystomum* are 15-20 μ in diameter, the zoospores 3-4 μ , and the broadest part of the vegetative system 3 μ . This agrees well with the sizes of these parts in Karling's *C. replicatum*. Hence, save for the occurrence of several discharge tubes and the lack of proliferated sporangia, Zopf's fungus appears nearly identical with Karling's. The multiplicity of tubes is not unknown in *C. replicatum* and may have been due in Zopf's

fungus to poor environmental conditions. Karling's name, however, is preferred, since the organism has been more completely described by him.

Shell-boring "Cladochytria"

Zebrowski (1936) and Porter and Zebrowski (1937) have lately described from bits of calcareous Australian sand of uncertain geological age, presumably from Cambrian to Recent, a number of so-called "lime-loving" fungi which are believed to be members of the Cladochytriaceae. Through the kindness of Mr. Zebrowski a number of slides of these sands have been examined. As the photographs accompanying his paper clearly indicate, the bits of shell have been bored through by some organism that has a saclike enlargement from which radiate delicate rhizoidal canals. These sacs, which are presumed to be sporangia, empty to the outside of the shell by a tube. In certain instances, as for example in *Dodgella priscus*, which was found in shells and also in spicules of calcareous sponges, sporelike structures were observed in the sacs. Such spores were also found imbedded in cavities of varying depth on the outer surface of bits of shells. As Zebrowski supposes, it is possible that the spores secrete a substance which allows them to penetrate or burrow into the matrix. Indeed, it is necessary that they secrete some lime-dissolving fluid if they are to maintain themselves in such a substratum.¹

It is obvious that the "fossil" nature and affinities of these forms must await the results of investigation on living material, which no doubt exists. Such investigation will be difficult because of the opaque nature of the substratum.

These shell-boring "fungi" have been known for a long time, and in 1860 Kölliker (1860a, 1860b) issued an extensive account of various "vegetable parasites" of shells, sponge spicules, scales of fishes, and the like. In Kölliker's paper references are found to still earlier investigations. As a result of his studies he concluded that the extraneous structures were fungi and noted that they were very frequent in marine organisms and almost or wholly lacking in freshwater forms. He also noted that not all marine animals were prey to the parasites, those with chitinous material being free of them. In the Mollusca, on the other hand, uninfected shells were the exception.

¹ Other slides kindly sent by Mr. Zebrowski show cavities shaped exactly like certain monocentric chytrids such as *Asterophlyctis*.

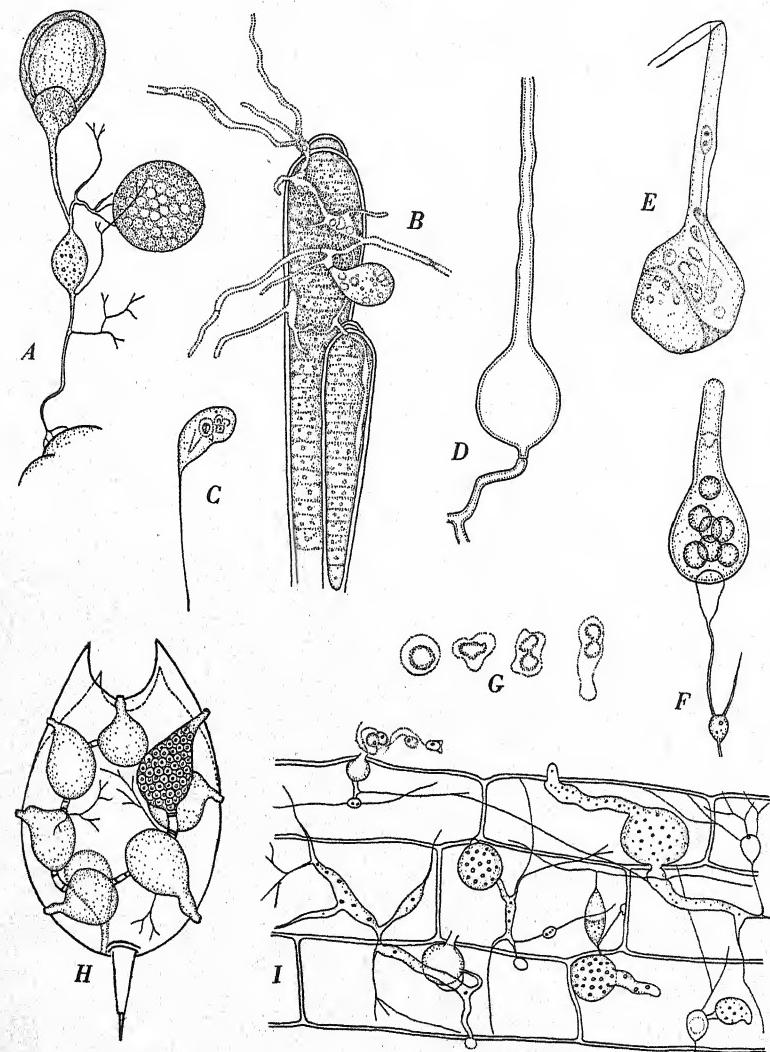


FIG. 20. Cladophytriaceae

A. *Physocladia obscura* Sparrow ($\times 580$), habit of plant on pollen grain; an immature sporangium and a terminal empty internally proliferous one are

Types with a thick periostracum and a prismatic layer were not attacked, the fungi evidently not being able to effect penetration. The shell-boring forms apparently accomplished their entrance by the secretion of an acid which dissolved the lime or, in the resistant sponge skeletons, possibly by mechanical action. Kölliker left open the question of whether they were algae or fungi, but was strongly inclined toward believing that they belonged to the latter group.

Opportunity was also afforded recently for examining sponge spicules with numerous canals in them. These were kindly sent by Dr. Arndt of the Berlin Zoological Museum. As in the shell-boring "Cladochytria," however, nothing could be definitely learned from prepared material concerning the affinities of these organisms. Until all of them have been studied in the living state and their spore structure determined little can be said of their relationships to the chytrids or, indeed, to the fungi.¹

PHYSOCLADIA SPARROW

Mycologia, 24:285. 1932

(Figure 20 A)

Thallus predominantly extramatrical, rhizoidal, much branched, polycentric, with septate turbinate cells and nonseptate fusiform or irregular swellings, bearing the rudiments of the sporangia and

shown. *B-E. Coenomyces consuens* Deckenbach on a marine species of *Calothrix*: *B*, habit of plant bearing single sporangium ($\times 372$); *C*, single zoospore with pale-yellow globule ($\times 2250$); *D*, empty sporangium with long discharge tube ($\times 330$); *E*, partly discharged sporangium; remaining contents and globules are pale yellow. *F-G. Amoebochytrium rhizidioroides* Zopf ($\times 540$) in slime sheath of *Chaetophora*: *F*, mature apophysate sporangium with globules of spores; septum in discharge tube is still present; *G*, some of shapes assumed by nonflagellated, amoeboid, spores. *H. Catenaria Anguillulae* Sorokin ($\times 370$) in body of rotifer; all but one sporangium has discharged its zoospores. *I. Cladochytrium tenuie* Nowakowski ($\times 500$) in decaying tissue of *Acorus Calamus*.

(*A*, Sparrow, 1931c; *B-E*, Deckenbach, 1903; *F-G*, Zopf, 1884; *H*, Sparrow, 1932b)

¹ Other fossil chytrids have recently been described by Daugherty (1941).

resting spores; sporangia inoperculate, terminal, proliferating; zoospores posteriorly uniflagellate, with a single globule, produced within the sporangium, liberated through a pore formed upon the deliquescence of a papilla and undergoing a period of swarming in a vesicle at the orifice before escaping; resting spores thick-walled, borne on the thallus, germination not observed.

Known thus far only as a saprophyte of the staminate cones of *Pinus*.

This monotypic genus resembles *Nowakowskia* very closely. It differs in having an inoperculate sporangium which forms a well-defined vesicle within which, upon discharge, the zoospores swarm before their escape.

PHYSOCLADIA OBSCURA Sparrow

Mycologia, 24:285, fig. 4e. 1932

(?) *Nowakowskia obscura* Sparrow, Amer. J. Bot., 18:621, pl. 45, figs. A-G. 1931.

Sporangia terminal, spherical or subspherical, apophysate, 42μ in diameter, with a thin brownish wall which wrinkles after discharge, plasma colorless, rhizoidal system variable, delicate, bearing numerous fusiform spherical and irregular swellings and occasionally septate turbinate cells; zoospores spherical, 4.2μ in diameter, with a centric colorless globule and a single flagellum, escaping upon the dissolution of an apical or subapical papilla into a broad flask-shaped vesicle in which they swarm; resting spores apparently terminal, on broad elements of the rhizoidal system, spherical, $21-50 \mu$ in diameter, with a dark-brown thick rough wall, contents granular, germination not observed.

Saprophytic in staminate cones of *Pinus*, in water culture containing *Sphagnum*, UNITED STATES.

The rhizoidal system which ramified between the pollen sacs and inside between the pollen grains possessed numerous irregularities and swellings. The extramatrical rhizoids which bore the sporangia were tenuous, with large nonseptate fusiform swellings.

AMOEBOCHYTRIUM ZOPF

Nova Acta Acad. Leop.-Carol., 47:181. 1884

(Figure 20 F-G, p. 314)

Thallus polycentric, eucarpic, consisting of a branched rhizoidal system bearing on it intercalary swellings; sporangia inoperculate, formed by enlargement of the body of the encysted zoospore or of the intercalary swellings of the rhizoids, cut off at maturity by cross walls from the vegetative system and often disarticulated; zoospores without flagella (always?), escaping by forcing one of the gelatinized cross walls, movement amoeboid; resting spores not observed.

A monotypic genus in the gelatinous sheath of *Chaetophora*.

No further observations on this genus appear to have been published since Zopf's original description. Further study may give a clearer idea of the sequence of development than is found in Zopf's paper. Zopf conjectures that flagellate zoospores may sometimes be formed. Nonflagellate spores have also been reported in *Sporophlyctis* and *Sporophlyctidium*.

AMOEBOCHYTRIUM RHIZIDIOIDES ZOPF

Nova Acta Acad. Leop.-Carol., 47:181, pl. 17, figs. 1-13. 1884

Sporangia relatively large, pyriform, basally apophysate with a more or less prolonged discharge tube which after disarticulation generally bears a short remnant of the concomitant rhizoid distally beyond the cross wall, wall stout, smooth, cuticularized, brownish; rhizoidal system extensive, branched, with occasional intercalary fusiform swellings; zoospores large, ovoid, with a large refractive yellowish globule, discharged through a pore formed in the cross wall which terminates the tubelike prolongation of the sporangium, movement strongly amoeboid; resting spores not observed.

Saprophytic on the gelatinous matrix of colonies of *Chaetophora elegans*, growing between the radiating algal branches, GERMANY.

SUBFAM. CATENARIOIDEAE

Vegetative system predominantly tubular and septate, with or without secondary rhizoidal axes.

CATENARIA SOROKIN

Ann. Sci. Nat. Bot., VI, 4:67. 1876

(Figure 20 H, p. 314)

Thallus endobiotic, eucarpic, predominantly strongly polycentric, branched or unbranched, septate, the septa delimiting the rudiments of the sporangia, resting spores, or sterile isthmuses; sporangia inoperculate, generally with a single discharge tube; zoospores posteriorly uniflagellate, with one or more globules, formed in the sporangium; resting spores thick-walled, borne like the sporangia, upon germination functioning as a sporangium.

Parasitic or saprophytic in the eggs of small or microscopic animals, *Anguillulae*, liver flukes, mites, adult rotifers, and so on; saprophytic in fresh-water algae.

Species of the genus develop highly specialized, often extensive polycentric thalli.

Considerable work has been done in recent years on *Catenaria Anguillulae* and much is known about its morphology and method of development. Sorokin stated that the young thallus was septate and that certain segments expanded to produce the sporangia. Others remained narrow and formed septate two-celled isthmuses. Dangeard (1884-85b), on the other hand, did not believe segmentation occurred until after the appearance of the branches and sporangial rudiments. He also detected the presence of the rhizoids and the lack of constancy of the two-celled character of the isthmus. Subsequent investigations by J. B. Butler and Buckley (1927), E. J. Butler (1928), Buckley and Clapham (1929), and Karling (1934a; 1938b) have indicated the correctness of the sequence described by Dangeard.

Although, as indicated above, *Catenaria* is found on a wide variety of substrata, the limits of the species both physiologically and morphologically are not as yet well established. From Karling's investigations, a single strain may be omnivorous and able to utilize as substrata a great many different plant and animal materials. The great variability in the shape and sizes of the parts of the thalli adds further to the taxonomic difficulties. Attempts to separate the species on the size and internal structure of the zoospore and the shape of the sporangia have yielded only partly satisfactory results. Other bases for distinction will have to be found, perhaps in the resting

spore. A resting body has been described by Buckley and Clapham (*loc. cit.*) in *C. Anguillulae* which rests loosely in the expanded part of the thallus. This structure is simply a sporangium the contents of which have contracted and become invested with a thick wall. A similar type of body has been found in *C. sphaerocarpa* by Karling (1938b) which, however, fills the containing structure. If these two bodies are indeed the resting spores, then *C. Anguillulae* may be distinguished from *C. sphaerocarpa* on a more satisfactory morphological basis than now exists.

KEY TO THE SPECIES OF CATENARIA

Zoospores 1.5–2 μ in diameter, with one or several globules

C. Anguillulae, p. 319

Zoospores 4–4.8 μ in diameter, with a single globule

C. sphaerocarpa, p. 320

CATENARIA ANGUILLULAE Sorokin

Ann. Sci. Nat. Bot., VI, 4:67, pl. 3, figs. 6–28. 1876

(Figure 20 H, p. 314)

Sporangia variable in shape, spherical, ovoid, oblong, triangular, or bursiform, extremely variable in size, up to 130 μ long by 50 μ in diameter or larger, discharge tube variable in length; isthmuses one- or two-celled, rhizoids delicate, branched, extensive or poorly developed; zoospores spherical, 1.5–2 μ in diameter, or elongate, 6–7 μ long by 4–5 μ wide, with one or several colorless globules, emerging individually and swimming directly away or forming a temporary group at the orifice; resting spores (?) spherical or irregularly ovoid, up to 65 \times 50 μ , thick-walled, each lying loosely in a sporangium-like structure, upon germination forming a discharge tube and functioning as a zoosporangium.

In exuviae of *Gordius spp.*, Villot (1874: pl. 6, figs. 13–18), *Anguillulae*, *Nitella*, Dangeard (1884–85b:126; 1886a:307, pl. 14, figs. 12–16), FRANCE; *Anguillulae*, Sorokin (*loc. cit.*; 1883:39, fig. 50), EUROPEAN RUSSIA, ASIATIC RUSSIA; *Anguillulae*, Constantineanu (1901:389, fig. 84), RUMANIA; nematodes, Seurat (1920:189), ALGERIA; eggs of *Fasciola hepatica*, J. B. Butler and Buckley (1927:497, pls. 23–26), E. J. Butler (1928:817, figs. 1–19), J. B. Butler and Humphries (1932:301, pls. 13–18), IRELAND; helminth and mite eggs, Buckley and Clapham (1929:1, pl. 1, figs. 1–21), ENGLAND; adult

rotifers, Sparrow (1932b:284, fig. 4h), roots of *Panicum* and sterilized green algae, characeans, liverworts, eggs of rotifers, Infusoria, insects, and so forth, Karling (1934a:528, figs. 1-3, pls. 57-58), UNITED STATES.

The fungus described in eggs of *Nais* by Carter (1858:99, pl. 4, fig. 45) probably belongs here.

The diagnosis above is admittedly unsatisfactory, and the species as it is now understood is probably a collective one. Significant data of taxonomic worth await the results of single zoospore cultures on a variety of living and dead animal and plant substrata. The species has been cultivated on artificial media by J. B. Butler and Humphries (1932).

Dangeard (1886a) identified *Catenaria Anguillulae* with *Chytridium zootocum* Braun, but this cannot be validated with certainty on the basis of Braun's description.

CATENARIA SPHAEROCARPA Karling

Amer. J. Bot., 25:328, text figs. 1-34. 1938

"Thallus predominantly polycentric, occasionally monocentric. Zoosporangia hyaline, smooth, usually spherical, 8-50 μ , oval, 8 \times 10 μ -30 \times 33 μ , and sometimes spindle-shaped, 7 \times 14 μ -15 \times 25 μ , with 1-3 straight, curved, or irregular exit tubes, 5-600 μ long and 2.5-4 μ in diameter, which may end flush with the surface of the host cell or extend 3-200 μ beyond it. Zoospores spherical, 4-4.8 μ with a single, large hyaline refractive globule; cilium approximately 25 μ long; emerging singly in succession and after a momentary pause swimming away. Isthmuses between sporangia of variable length, rarely inflated and spindle-shaped. Rhizoids numerous, well developed and branched, arising from the isthmuses as well as from the sides and ends of the sporangia. Resting spores usually spherical and oval, 10-25 μ , occasionally spindle-shaped and elongated with a heavy brown wall 1.5-2.5 μ thick, and an evenly granular content; apparently developed in the same manner as the zoosporangia; germination unknown" (Karling, loc. cit.).

Saprophytic in dead and cooked cells of *Hydrodictyon reticulatum*, *Chara coronata*, *Nitella flexilis*, *Cladophora glomerata*, *Pithophora* sp., *Spirogyra crassa*, *Anacharis canadensis*, and root tips of *Zea mays* and *Allium cepa*, Karling (loc. cit.), dead *Cladophora*, Sparrow (MICHIGAN), UNITED STATES.

COENOMYCES DECKENBACH

Scripta Bot. Horti Univ. Imper. Petro., 19:15. 1902-3; Flora, 92:265.
1903

(Figure 20 B-E, p. 314)

Thallus epi- and endobiotic, eucarpic, consisting of a filamentous branched segmented loose hypha-like complex of tubes bearing occasional irregular intercalary swellings; sporangia inoperculate, borne extramatrically at the tips of hyphal branches or occasionally sessile on the host cell; zoospores posteriorly uniflagellate, emerging fully formed through a single (rarely more than one) long discharge tube; resting spores not observed.

A monotypic genus known only in gelatinous material of blue-green algae.

Jaczewski (1931:32) has proposed a new generic name, *Deckenbachia*, nom. nov., for *Coenomyces*. The reasons for this change are not given in the Russian text, but presumably the name *Coenomyces* is preëmpted and is therefore a homonym.

COENOMYCES CONSUENS Deckenbach

Scripta Bot. Horti Univ. Imper. Petro., 19:15, pls. 1-2. 1902-3;
Flora, 92:265, pls. 6-7. 1903

Mycelium divided by cross walls into long segments, much branched extramatrically and bearing frequent irregular swellings, the endobiotic part less branched, lying between the cells and the sheath of the alga, with occasional swollen appressoria; sporangia pyriform, ovoid, or bursiform, 15-22.5 μ in diameter by 21-24.7 μ long, with a cylindrical attenuated discharge tube (rarely two) 120-153 μ long by 6 μ in diameter, tapering to 2 μ at the tip, wall thin or somewhat thickened; zoospores ellipsoidal or pyriform, 1.5 μ in diameter, with a long flagellum and golden-yellow contents.

In the jelly and between the cells of *Calothrix* sp., Deckenbach (*loc. cit.*), RUSSIA (marine); *Calothrix parasitica*, W. H. Weston, Jr., and D. M. Reynolds, *Rivularia atra* var. *confluens*, I. Lewis and Weston, UNITED STATES (all previously unpublished records for this country).

Petersen (1906) has reported finding this species in fresh-water blue-green algae in Denmark.

Little is known about the development of the species save that the zoospore upon germination produces two oppositely directed germ tubes. The cross walls in the species do not occur at such frequent intervals as do those of the higher fungi, but rather separate the hyphae into a series of fairly long cylindrical segments. The fungus is remarkable in the possession of a definitely hypha-like vegetative system and chytridiaceous zoospores. There appears to exist an operculate counterpart of *Coenomyces* (see Sparrow, 1936a: 432, pl. 15, figs. 22-23) which inhabits decaying twigs in fresh water.

To afford a resting place for his extraordinary fungus Deckenbach erected the "Coenomycetes," filamentous fungi with a septate mycelium, reproducing by zoospores.

IMPERFECTLY KNOWN GENERA OF THE CLADOCHYTRIACEAE

? NEPHROMYCES GIARD

C. R. Acad. Sci. Paris, 106:1180. 1888

Vegetative system in the kidney of ascidians, composed of coenocytic strongly entangled delicate filaments, the free ends terminated by spheroidal swellings, bearing irregularly cylindrical contorted intercalary swellings which become the inoperculate sporangia; zoospores minute, spherical, with a basal granule and a long delicate flagellum; zygospores formed by conjugation of from four to five filaments, granular or slightly echinulate, upon germination giving rise to two opposite germ tubes.

The affinities of the genus cannot be ascertained until further observations have been made. Recently Harant (1931:349) has discussed *Nephromyces* in the kidney of *Ctenicella appendiculata*. However, it still remains a puzzling organism. Giard allies it to *Catenaria*.

Three species are described from France:

Nephromyces Molgularum in *Molgula socialis*;

Nephromyces Sorokini in *Listhonephrya*, with regularly pyriform sporangia;

Nephromyces Roscovitanus in *Anurella*.

From what is known about these fungi it is evident that in this curious habitat—the ductless kidney of certain, perhaps all, marine ascidians—there may be a sort of commensalism which will repay careful investigation.

? SACCOPODIUM SOROKIN

Hedwigia, 16 (6):88, figs. 1-3 (lower plate). 1877¹

Thallus tubular, without cross walls, branched, endobiotic with extramatrical unbranched sporangiophores; sporangia in clusters of from six to twelve at the tips of the extramatrical sporangiophores, spherical or pyriform, 4-5 μ in diameter, without a discharge tube; zoospores oblong, 1-1.5 μ (long?), emerging through an opening in the sporangium, flagella not observed; resting spore not observed.

A monotypic genus, represented only by *Saccopodium gracile* on *Cladophora*, ASIATIC RUSSIA.

Recent incomplete observations on a fungus on *Cladophora* collected in Michigan have convinced the present author that there exists a chytrid in which the sporangia occur in clusters at the tip of an extramatrical tubular sporangiophore. There were certain differences, however, particularly the apophysate character of the zoosporangia, which make it impossible to identify the Michigan fungus with Sorokin's.

OPERCULATAE

CHYTRIDIACEAE

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part either expanding and forming an operculate sporangium and the endobiotic part forming the vegetative system, or not enlarging and forming an evanescent cyst, the endobiotic part then forming the reproductive organs as well as the vegetative system; zoospores produced in the sporangium, posteriorly uniflagellate, generally with a single globule, released upon the dehiscence of the operculum; sexual reproduction, where known, by fusion of aplanogametes; resting spore upon germination producing an epibiotic sporangium.

Primarily parasites and saprophytes of fresh-water and marine algae and, with the inoperculate Phlyctidiaceae, making up the major-

¹ In *Arch. Bot. Nord France*, 2:23, 1883, there appears another figure (Fig. 21), not found in the 1877 paper.

ity of the "chytrids." The family includes the operculate counterparts of the Phlyctidiaceae, a remarkable parallelism in body form being recognizable in the two series. Species of the largest genus, *Chytridium*, with apophyses and those with unbranched rhizoidal systems have never been segregated into distinct genera as have parallel forms in the Phlyctidiaceae.

**KEY TO THE SUBFAMILIES AND GENERA OF THE
CHYTRIDIACEAE**

Sporangium epibiotic; resting spore endo- or epibiotic

Sporangium formed by expansion of the whole body of the encysted zoospore or, if not, the spore case continuous with the sporangium; rhizoids delicate; plants minute

Resting spore endo- or epibiotic, apparently asexually formed, apophysis, if present, single or catenulate

Subfamily CHYTRIDIOIDEAE, p. 324

Sporangium with or without a simple apophysis; resting spore endobiotic

CHYTRIDIUM, p. 325

Sporangium with a compound, catenulate apophysis, resting spore epi- or endobiotic

CATENOCHYTRIDIUM, p. 362

Resting spore epibiotic, formed after a process of aplanogamic sexual reproduction, apophysis simple

Subfamily ZYGORHIZIDIOIDEAE, p. 363

ZYGORHIZIUM, p. 363

Sporangium or resting spore formed as a lateral walled-off outgrowth of the distal part of the cylindrical main axis; rhizoids broadly tubular, extensive; the whole plant large

Subfamily MACROCHYTRIOIDEAE, p. 365

MACROCHYTRIUM, p. 365

Sporangium and resting spore endobiotic; epibiotic part evanescent

Subfamily ENDOCHYTRIOIDEAE, p. 368

Sporangium without an apophysis

ENDOCHYTRIUM, p. 368

Sporangium with an apophysis

NEPHROCHYTRIUM, p. 374

SUBFAM. CHYTRIDIOIDEAE

Sporangium epibiotic, sessile; rhizoids endobiotic, delicate, tapering; resting spore endo- or epibiotic, apparently asexually formed.

CHYTRIDIUM BRAUN

Betrachtungen über die Erscheinung der Verjüngung in der Natur . . .,
p. 198. Leipzig, 1851; Monatsber. Berlin Akad., 1855:378

(Figure 21 A-Q, p. 330)

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming the rudiment of the sporangium, the endobiotic part producing the vegetative system and resting spore; sporangium epibiotic, sessile, operculate, formed from all or part of the enlarged body of the encysted zoospore; zoospores posteriorly uniflagellate, usually with a single globule; rhizoidal system endobiotic, variable in character, arising either from the endobiotic tip of the germ tube or a prolongation of it or from an endobiotic subsporangial apophysis; resting spore endobiotic, thick-walled, often borne on a rhizoidal system, apparently asexually formed, upon germination producing an epibiotic operculate zoosporangium.

Primarily parasites and saprophytes of fresh-water algae.

Braun's subgeneric term *Euchytridium* has been used occasionally in a generic sense, notably by Sorokin (1883).

As understood here, *Chytridium* includes all monocentric, eucarpic chytrids, with or without a simple apophysis, which form an epibiotic sporangium, discharge their spores after the dehiscence of a single operculum, and have endobiotic resting spores. The nature of the rhizoidal system produced by different species of the genus is extremely variable and ranges from a delicate apparently unbranched needle-like tube in *C. Lagenula* to the broad often apophysate tubular structure divided distally into tenuous branched rhizoids found in *C. olla*. An exception to the endobiotic nature of the rhizoid is found in *C. curvatum*, where the tip of the short subsporangial stalk evidently does not penetrate beyond the thin layer of gelatinous material surrounding the *Stigeoclonium* filament.

Segregation from *Chytridium* of the species with an unbranched rhizoid or with a subsporangial apophysis has never been made, as it has among the inoperculate species formerly grouped under *Rhizophyridium* (*Phlyctidium*) and *Rhizidium* in the sense of Fischer (*Phlyctochytrium*).

Scherffel (1925b:7) has suggested that *Zygorhizidium Willei*, with *Chytridium*-like operculate sporangia and epibiotic resting spores

be included in a new subgenus of *Chytridium*, *Ectochytridium*. In view of the type of sexuality which occurs in *Zygorhizidium* (see p. 53) it would appear better to retain Löwenthal's genus as a distinct one until more is known of the sexual process, if any, in *Chytridium*. Fisch (1884b) describes copulation of motile bodies preceding the formation of endobiotic resting spores in "*Chytridium Mesocarpi*"; the correctness of his account has been questioned by both Fischer and Minden. Neither, however, notes that Fisch's fungus produced *anteriorly* uniflagellate zoospores and hence was no *Chytridium* (see p. 360).

The curious expansion of only a portion of the cyst of the infecting zoospore in *Chytridium Schenkii* and related species was first noted by Schenk.

KEY TO THE SPECIES OF CHYTRIDIUM

Occurring in fresh-water or inland salt pools

Rhizoids arising directly from the tip of the penetration tube,
branched or unbranched

Rhizoids branched or, if unbranched, tapering and delicate

Sporangium ovoid or urceolate at maturity

Sporangium ovoid or narrowly urceolate, with a rounded
base; operculum usually umbonate; on green algae

Sporangium 11-100 μ high by 6-55 μ in diameter;
umbo, when present, not prolonged *C. olla*, p. 328

Sporangium smaller, about 16 μ in diameter; umbo
distinct and prolonged *C. acuminatum*, p. 331

Sporangium broadly urceolate with a concave base;
operculum smoothly convex, 20 μ in diameter; on
cysts of *Vampyrella* *C. lateoperculatum*, p. 332

Sporangium distinctly pyriform, citriform, obpyriform, or
pestle-shaped

Sporangium pyriform or citriform

Sporangium distinctly pyriform; rhizoidal axis elongate

Sporangium predominantly narrowly pyriform,
asymmetrical (tilted); operculum inconspicuous;
rhizoids tenuous; on *Conjugatae*

C. sphaerocarpum, p. 332

Sporangium broadly and symmetrically pyriform;
operculum conspicuous, solid; rhizoids stout;
on diatoms *C. perniciosum*, p. 333

Sporangium pyriform to citriform; rhizoidal axis
short; on *Stigeoclonium* *C. papillatum*, p. 334

- Sporangium obpyriform or pestle-shaped
 - Sporangium obpyriform
 - Sporangium with a knoblike or slightly prolonged base, borne on a slender flexible extramatrical stalk; on diatoms *C. versatile*, p. 334
 - Sporangium gradually tapering basally, sessile; on *Vaucheria* *C. pyriforme*, p. 335
 - Sporangium pestle-shaped, sessile or with a short tenuous extramatrical stalk; on *Tribonema* *C. Lagenula*, p. 336
- Rhizoids, where known, unbranched, isodiametric
 - Sporangium wall smooth
 - Sporangium sessile, thin-walled, narrowly to broadly obpyriform, procumbent, rhizoids completely endobiotic *C. appressum*, p. 337
 - Sporangium borne on a short epibiotic stalk, strongly arched, basal part thick-walled and sterile
 - C. curvatum*, p. 337
 - Sporangium wall ornamented
 - Sporangium with an apiculus or nodular protuberance on upper part
 - Sporangium with an apiculus; operculum subapical
 - C. Epithemiae*, p. 338
 - Sporangium with a small subapical nodular protuberance; operculum apical *C. nodulosum*, p. 338
 - Sporangium bearing long setae or short conical spines
 - C. chaetophilum*, p. 339
- Rhizoids arising from a well-defined endobiotic subsporangial swelling (apophysis)
 - Sporangium with two opposed solid apical teeth; rhizoids broad, isodiametric, arising from opposite sides of a transversely fusiform apophysis *C. Confervae*, p. 340
 - Sporangium without apical teeth; rhizoids tapering, apophysis variable in shape
 - Sporangium wall with part of the case of the zoospore persisting as a small hemispherical refractive or colored protuberance
 - Sporangium ovoid, ellipsoid, pyriform, or subspherical; protuberance colorless, or amber or brown
 - Protuberance colorless
 - Sporangium ovoid, ellipsoid, or pyriform; protuberance basal or slightly elevated; operculum small; rhizoids branched, tapering *C. Schenkii*, p. 342
 - Sporangium narrowly obovoid; protuberance basal; operculum small; rhizoid tubular and unbranched *C. Oedogonii*, p. 343

- Sporangium spherical, subspherical, or ellipsoidal; protuberance subapical or lateral; operculum large *C. Kolianum*, p. 344
- Protuberance amber or brown; sporangium ovoid or subspherical *C. aggregatum*, p. 344
- Sporangium utriculate or somewhat tubular, dorsally gibbose; protuberance colorless *C. gibbosum*, p. 345
- Sporangium wall entirely smooth
- Sporangium broadly obovoid, often asymmetrical; apophysis spherical, without rhizoids *C. Scherffelii*, p. 346
- Sporangium spherical, subspherical, ovoid, urceolate, or pyriform
- Sporangium broadly pyriform or urceolate; operculum prominent, strongly convex; apophysis spherical, apparently without rhizoids *C. inflatum*, p. 346
- Sporangium spherical, subspherical, ovoid, urceolate, or pyriform; operculum slightly convex; apophysis spherical or otherwise
- Apophysis spherical, without rhizoids; operculum generally umbonate *C. breipes*, p. 347
- Apophysis spherical, subspherical, flattened, fusiform, or broadly tubular; rhizoids extensive, stout; operculum smooth *C. Lagenaria*, p. 348
- Occurring in marine waters
- Rhizoids branched, broad, often swollen or vesiculate or consisting of two saccate branches; on *Codium* *C. codicola*, p. 351
- Rhizoids branched or unbranched, delicate
- Sporangium subspherical, subangular, pyriform, or urceolate; pore apical *C. Polysiphoniae*, p. 351
- Sporangium obpyriform; pore large, generally subapical
- C. megastomum*, p. 352

CHYTRIDIUM OLLA Braun

Betrachtungen über die Erscheinung der Verjüngung in der Natur . . . , p. 198.
 Leipzig, 1851; Monatsber. Berlin Akad., 1855:380; Abhandl.
 Berlin Akad., 1855:23, pl. 1, figs. 1-10. 1856
 (Figure 21 A, p. 330)

Euchytridium olla (Braun) Sorokin, Arch. Bot. Nord France, 2:21, fig. 19. 1883 (separate).

Sporangium sessile, rarely stalked, ovoid or somewhat urceolate, 11.9-100 μ high by 10.6-55 μ in diameter, the apex terminated by a

broad convex umbonate or occasionally smooth operculum 7–14 μ in diameter, wall smooth, colorless, of varying thickness; rhizoids tenuous and much branched within the host contents, arising from a broad often irregularly expanded tubular endobiotic occasionally septate stalk of variable length, which originates at the base of the sporangium but is cut off from it by a cross wall at maturity; zoospores up to several hundred in large sporangia, spherical, 3.3–5 μ in diameter, with a colorless eccentric globule and a flagellum from four to six times the length of the diameter of the body, emerging individually or in a group imbedded in "slime" and remaining motionless for a time, movement hopping, amoeboid; resting spore formed on the endobiotic system, spherical, subspherical, or occasionally pyriform, 24–32.4 μ in diameter, wall smooth, thick, contents with a single large oil globule, upon germination producing an epibiotic operculate sporangium.

On oögonia and oöspores of various species of *Oedogonium*, Braun (*loc. cit.*), (coll. Pringsheim) Braun (1856a:23), Kny (1871a: 870), de Bary (1884:177, fig. 76), GERMANY; Sorokin (1874b:8, pl. 1, figs. 29–40; 1883:21, fig. 19), Serbinov (1907:77, pl. 5, figs. 9–10), Voronichin (1920:11), EUROPEAN RUSSIA; (coll. Haussknecht) Rabenhorst (1871:17), ASIATIC RUSSIA; Tokunaga (1934b:392), JAPAN; oögonia of *Nitella tenuissima* (?), Sparrow (1936a:430, pl. 15, figs. 1–11), ENGLAND.

Since this species is the unquestioned type of the genus, although apparently not the first chytrid observed by Braun (see *Phlyctochytrium Hydrodictyi*), it is of unusual importance. In it are embodied not only the characters of a *Chytridium*, but also those which to a degree must be exhibited by all "chytrids." As noted in the diagnosis of the order, these center around the structure of the zoospore.

The sporangia are extremely variable in size, a fact first pointed out by Kny, who found them ranging from 11.9–100 μ high by 10.6–55 μ in diameter. The more proximal portion of the rhizoidal system is apparently subject to considerable variation, sometimes being evenly tubular and sometimes expanded into an irregular or rounded apophysis. Occasional septations may also occur. Observations on the nature of the rhizoids are difficult within the host contents. Both Serbinov and Sparrow have confirmed the fact, first noted with uncertainty by Braun (1856a:25), that distally the rhizoid becomes divided into a number of more delicate tapering branches.

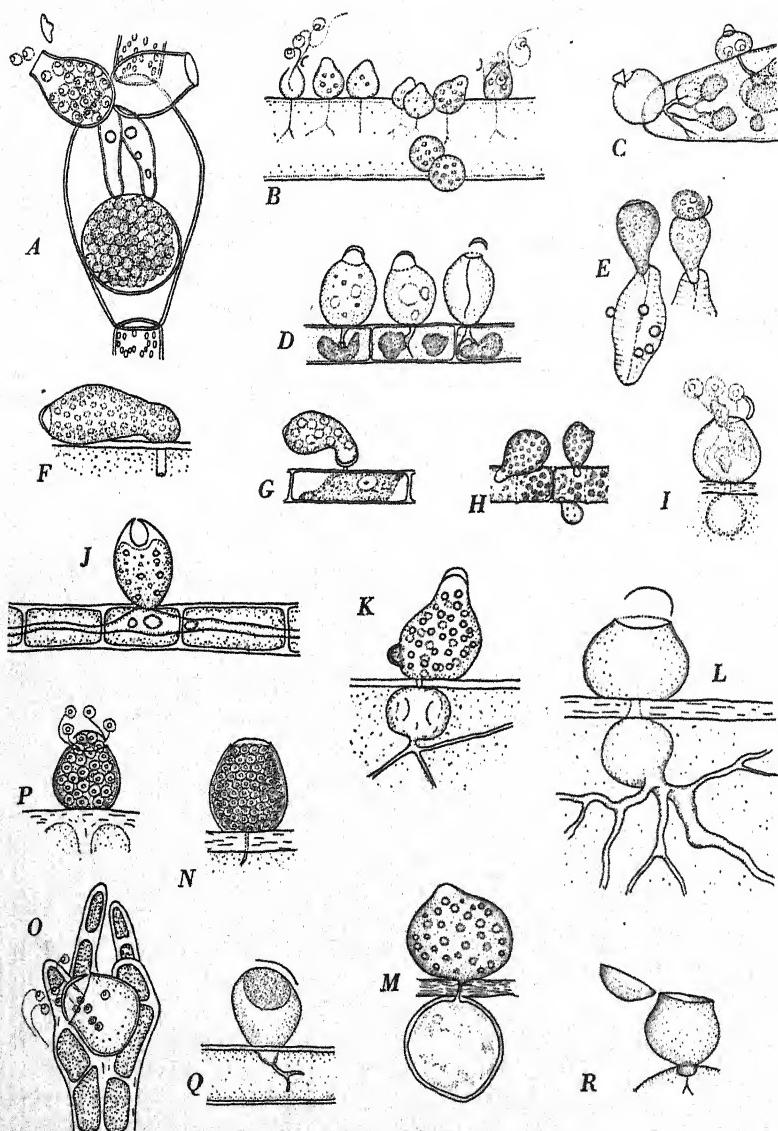


FIG. 21. Chytridiaceae

The curious production of flamelike refractive outgrowths of the sporangium wall has been noted by Sparrow (*loc. cit.*).

CHYTRIDIUM ACUMINATUM Braun

Monatsber. Berlin Akad., 1855:380; Abhandl. Berlin Akad., 1855:29, pl. 1,
fig. 11. 1856

Sporangium sessile, ovate, ovate-pyriform, or urceolate, 16.6μ high, with a distinctly umbonate operculum, wall smooth, colorless;

Explanation of Figure 21

A. *Chytridium olla* Braun ($\times 200$) on oögonium of *Oedogonium*, two discharged sporangia. B. *Chytridium sphaerocarpum* Dangeard ($\times 550$) on hypha of *Achlya*. C. *Chytridium perniciosum* Sparrow ($\times 375$) on *Navicula*, two discharged sporangia on portion of diatom. D. *Chytridium papillatum* Sparrow ($\times 760$) on *Stigeoclonium*, immature and discharged sporangia on portion of algal filament. E. *Chytridium versatile* Scherffel on moving *Navicula*; to the left, five encysted zoospores and a mature sporangium on its flexible stalk; to the right, a discharging sporangium. F. *Chytridium appressum* Sparrow ($\times 1300$) on *Melosira*, habit of a mature sporangium. G. *Chytridium curvatum* Sparrow ($\times 600$) on sheath of *Stigeoclonium*. H. *Chytridium nodulosum*, sp. nov. ($\times 450$), on *Melosira*, three sporangia, the one in upper right showing characteristic protuberance (zoospore case?). I. *Chytridium inflatum* Sparrow ($\times 600$) on *Cladophora*, discharging apophysate sporangium. J. *Chytridium Confervae* (Wille) Minden ($\times 630$), immature sporangium on *Tribonema*. K. *Chytridium aggregatum* Karling ($\times 740$) on *Cladophora*, single apophysate sporangium from a group; persistent amber-colored case of zoospore appears as protuberance on left side of sporangium wall. L-M. *Chytridium Lagenaria* Schenk on *Rhizoclonium* and *Oedogonium*: L, empty apophysate sporangium ($\times 400$); M, germinating resting spore on *Oedogonium*; endobiotic resting spore has produced a germ tube, which has pierced wall of alga and formed at its tip, epibiotically, a zoosporangium. N-P. *Chytridium Polysiphoniae* Cohn on the seaweeds *Polysiphonia* and *Ceramium*: N, mature sporangium ($\times 570$) on *Ceramium*; O, discharging sporangium ($\times 376$) on *Polysiphonia*; P, discharging sporangium ($\times 570$) on *Ceramium*. Q. *Chytridium megastomum* Sparrow ($\times 570$), empty sporangium on hairs of the brown seaweed *Striaria*. R. *Zygorhizidium Willei* Löwenthal ($\times 1125$) on *Cylindrocystis*, empty sporangium, showing small endobiotic apophysis and once-branched rhizoid.

(A, Braun, 1856a; B, Sparrow, 1936a; C-D, Sparrow, 1938c; E-I, Sparrow, 1938a; L, Sparrow, 1936a; M, Karling, 1936a; N, Sparrow, 1934c; O, Sparrow, 1936b; P-Q, Sparrow, 1934c; R, Löwenthal, 1905)

rhizoids and zoospores not observed; resting spore endobiotic, spherical, smooth-walled, with a single globule.

On oögonia of *Oedogonium Rothii*, possibly also on *O. echinospermum*, Braun (*loc. cit.*), GERMANY; diatoms, Sorokin (1883:21, fig. 18), ASIATIC RUSSIA; zygosporangia of *Mesocarpus*, Cornu (1872a:121), FRANCE.

Differing from *Chytridium olla* in the smaller size of its sporangia and the more pronounced umbo on the operculum. Though considered by Fischer and Minden to be only a small variety of *C. olla*, with a prolonged umbo, further observations should be made on the fungus before it is reduced to synonymy. "*Chytridium acuminatum*" of Scherffel (1926a:225), because of the formation of an endobiotic swelling, appears closer to *C. brevipes* Braun. Figures of the species are given in Cooke (1882-84:pl. 81, fig. 1).

CHYTRIDIUM LATEOPERCULATUM Scherffel

Arch. Protistenk., 54:173, pl. 9, fig. 10. 1926

Sporangium sessile, broadly and symmetrically urn-shaped, 12μ high by 20μ wide, with a smooth colorless wall, its broad concave base resting on the rounded wall of the host, opening with a sharply circular split at the dehiscence of a slightly convex large disclike operculum 20μ in diameter; zoospores and endobiotic system not seen; resting spore not observed.

On zoocyst of *Vampyrella pendula*, causing marked disorganization and clumping of the host contents, HUNGARY.

CHYTRIDIUM SPHAEROCARPUM Dangeard

Le Botaniste, 2:244, pl. 17, fig. 9. 1890-91

(Figure 21 B, p. 330)

Sporangium sessile, narrowly or occasionally broadly pyriform, usually asymmetrical, $8-18 \mu$ long by $7-8 \mu$ in diameter, with a prominent apical papilla surmounted by a very inconspicuous thin-walled convex operculum $3-5 \mu$ in diameter, wall thin, smooth, colorless; rhizoidal system of varying length, consisting of an extremely tenuous long stalk which forms at its tip a few branches or remains unbranched; zoospores spherical, $2.5-5 \mu$ in diameter, with a colorless

centric globule and a fairly long flagellum, escaping fully formed after the dehiscence of the operculum; resting spore not observed.

On *Zygnema* sp., Dangeard (*loc. cit.*), FRANCE; *Spirogyra* sp., *Stigeoclonium* sp., Sparrow (1933a:64, text fig. 1 g-i), UNITED STATES; *Spirogyra* sp., *Mougeotia* sp., *Achlya* (?), Sparrow (1936a, fig. 3 a-f), ENGLAND.

Dangeard identified his fungus with *Rhizidium sphaerocarpum* Zopf (*Rhizophydiump sphaerocarpum* (Zopf) Fischer), but placed it in *Chytridium* because of the lack of a basal cell (a feature of *Rhizidium* in the sense of Fischer) rather than because of the presence of an operculum.

The species is a difficult one to characterize, but its principal features are a narrowly pyriform sporangium, often appearing tilted (asymmetrical), an extremely delicate operculum, and a long rhizoid which sometimes forms a few branches at its tip. The chytrid on *Mougeotia* does not conform in this last detail, since the rhizoids branch near the host wall. Perhaps it should not be included here. Morphologically, the fungi found on *Spirogyra* and *Stigeoclonium* are indistinguishable from the fungus on *Achlya*.

CHYTRIDIUM PERNICIOSUM Sparrow

Mycologia, 25:526, pl. 49, figs. 9-11. 1933

(Figure 21 C, p. 330)

Sporangium sessile, smooth-walled, spherical at first, becoming broadly pyriform, 10-16 μ high by 12-23 μ in diameter (up to 30 \times 35 μ), with a prominent apical solid operculum which, upon discharge of the zoospores, remains attached to the sporangium and often falls back into place, covering the orifice; zoospores spherical, 3-4 μ in diameter, posteriorly uniflagellate, with a colorless globule; rhizoids stout, branching; resting spore spherical, 11-16 μ in diameter, endobiotic, with a smooth somewhat thickened wall and one or more large oil globules.

Parasitic on *Navicula* sp., UNITED STATES.

Large sporangia, about 30 μ high by 35 μ in diameter, were occasionally observed. Other, possibly abnormal, ones, ovoid, pyriform, or irregular in shape, with very thick walls and a hornlike broadly conical operculum, were also found. The fungus was an

extremely virulent parasite and destroyed within a few days nearly all the diatoms present in the dish. After being attacked the chloroplasts of the alga rapidly became discolored and desiccated. In immature sporangia the operculum often appeared invaginated. Such a condition has also been observed in *Blastocladia* and *Nawakowskia* and has been discussed by Scherffel (1926a:226), who unquestionably correctly assigns to it a function in zoospore discharge.

CHYTRIDIUM PAPILLATUM Sparrow

Mycologia, 25:525, text fig. I, 7. 1933

(Figure 21 D, p. 330)

Sporangium sessile, pyriform to citriform, 10-11 μ high by 7-8 μ in diameter, smooth-walled, with a prominent broad apical papilla surmounted by a convex operculum; rhizoidal system short, delicate, sparsely branched, arising from a stouter endobiotic subsporangial stalk; zoospores spherical, about 3-4 μ in diameter, posteriorly uniflagellate, with a colorless globule; resting spore not observed.

On filaments of *Stigeoclonium* sp., UNITED STATES.

In the shape of its sporangium and the nature of its rhizoidal system the organism is exactly like *Rhizophyidium mammillatum* (Br.) Fischer. From the accounts of Braun, Sorokin, Dangeard (as *Chytridium asymmetricum*), and Couch, however, *R. mammillatum* is inoperculate (see p. 177). Whether or not the fungus found by Pringsheim (reported in Braun, 1856a:33, pl. 2, figs. 9-11) on *Stigeoclonium* was a *Chytridium* or a *Rhizophyidium* cannot now be determined, since no discharge of the zoospores was observed.

CHYTRIDIUM VERSATILE Scherffel

Arch. Protistenk., 54:177, pl. 9, figs. 17-20. 1926

(Figure 21 E, p. 330)

Sporangium narrowly to broadly obpyriform, tapering proximally to a knoblike or slightly prolonged base 3-5 μ in diameter, resting on a short (3.5 μ) slender flexible extramatrical stalk, wall smooth, colorless, thin or somewhat thickened, variable in size, large specimens up to 15-25 μ in diameter by 30-40 μ high, smaller ones 5 \times 8 μ ; rhizoids extremely delicate, branched, arising from the endobiotic tip of the stalk; zoospores spherical, 3-5 μ in diameter, with a relatively large colorless centric globule and a long flagellum, emerging upon the dehiscence of an apical convex smooth operculum 8-10 μ in diameter

and forming a temporary motionless group surrounded by an evanescent vesicle or "slime"; resting spore not observed.

Parasitic on motile *Cymatopleura solea*, Scherffel (*loc. cit.*), *Melosira varians*, Domján (1936:pl. 1, fig. 110), HUNGARY; *Navicula* sp., Sparrow (1933a:63, text fig. 1 a-c, m), UNITED STATES; *Synedra* sp. (?), *Tabellaria* sp., Sparrow (1936a:437, fig. 3 g, t, fig. 4a), ENGLAND.

A curious adaptation of this fungus to its mode of life on moving diatoms has been pointed out by Scherffel (see under "Structure of the Thallus," p. 30).

Scherffel has noted that the method of development of the sporangium in this species is similar to that found in *Podochytrium*. The body of the original zoospore persists, unexpanded, as the knob-like base, while the remainder of the sporangium is formed by elongation and expansion of the apical part. In contrast to *Podochytrium*, however, the base remains continuous with the rest of the sporangium. In the Hungarian material no rhizoids were found within the host, and this, together with the fact that several fungi were present in various stages of development on moving diatoms, suggested to Scherffel that the adherent organism might be only a saprophyte on the gelatinous coating. Later observations (Sparrow, 1933a), indicated, however, that a true endobiotic system was developed and that the fungus might ultimately destroy its host.

Chytridium Lagenulá Braun, *sensu recent.* Scherffel, appears to differ from this species only in its host, in its smaller size, and in the somewhat broader base of the sporangium.

CHYTRIDIUM PYRIFORME Reinsch

J. Linn. Soc. London (Bot.), 15:215. 1877

Zoosporangium obpyriform, gradually narrowing toward the base, 26-28 μ high by 13-17 μ in diameter, wall distinctly thickened; rhizoids tapering; zoospores subcylindrical or subcuneate, ejected upon the dehiscence of an apical convex smooth operculum.

In *Vaucheria sessilis* and *V. geminata*, coll. Eaton, KERGUELEN ISLAND.

Shape said to approximate that of *Chytridium olla*, a statement hardly borne out by the description. The lack of figures makes the interpretation of this species difficult.

CHYTRIDIUM LAGENULA Braun, pro parte

Abhandl. Berlin Akad., 1855:31, pl. 2, figs. 4-5 (sensu recent. Scherffel,
Arch. Protistenk., 54:195, pl. 9, figs. 57-59. 1926)

Phlyctidium Lagenula (Braun) Rabenhorst, pro parte, Flora Europaea
algarum, 3:280. 1868.

Rhizophyridium Lagenula (Braun) Fischer, Rabenhorst. Kryptogamen-Fl.,
1 (4):99. 1892.

Sporangium sessile or with a short tenuous extramatrical stalk, narrowly obpyriform (pestle-shaped), with rounded apex, upright or slightly tilted, with a thin smooth wall, varying in size, large specimens 12-14 μ long by 5.5 μ in diameter, small ones 7 μ long by 4 μ in diameter; rhizoidal system not seen, the penetration tube stimulating the host to form a protective plug of wall material; sporangium opening upon the dehiscence of an arched apical operculum about 4 μ in diameter; zoospores few, spherical, 3 μ in diameter, with a single globule and probably a single flagellum, remaining motionless for a time at the mouth of the sporangium before swimming away; resting spore endobiotic, broadly ovoid or nearly spherical, 6-8 \times 5 μ , with a thick smooth wall and a large eccentric colorless oil drop 4 μ in diameter, germination not observed.

On *Tribonema bombycina*, Braun (*loc. cit.*), GERMANY; Scherffel (*loc. cit.*), HUNGARY; Sparrow, UNITED STATES (MICHIGAN).

Scherffel believes his fungus to be a new species, but since he describes a form almost identical with Braun's plant on *Tribonema* and applies Braun's name to it, it is here considered merely an amplification of a previously inadequately defined species. He believes Braun's *Chytridium Lagenula* to be divisible into two species, which differ in the size, the shape, and the method of opening of the sporangium, and in the behavior of the zoospores and the hosts: (1) *Rhizophyridium Lagenula* (Braun) Fischer on *Melosira*, which has a somewhat fusiform inoperculate sporangium 30-33 μ long by 8 μ in diameter and a zoospore, with a very small globule, escaping at once from the sporangium; and (2) *Chytridium Lagenula* Braun *sensu* Scherffel on *Tribonema*, which has a more clavate operculate sporangium 12-20 μ long by 5.5-8 μ in diameter, the zoospore having a larger globule and resting for a time before the mouth of the sporangium before assuming motility. He does not think *R. fusus* Zopf is synonymous with *R. Lagenula* (Braun) Fischer, but gives no reasons for

this opinion. See *R. fusus* (p. 202). Schenk (1858a:236) has reported it on *Stigeoclonium* in Germany.

The smaller form has frequently been found in early spring near Ann Arbor, Michigan, parasitizing *Tribonema bombycina*.

CHYTRIDIUM APPRESSUM Sparrow

Amer. J. Bot., 20:69, text fig. 1p. 1933

(Figure 21 F, p. 330)

Sporangium sessile, narrowly to broadly obpyriform, slightly constricted toward the base, 10–17 μ long by 6–10 μ in diameter, the long axis parallel with that of the algal filament, with a smooth colorless wall; endobiotic part consisting of a highly refractive narrowly cylindrical unbranched tube about 3 μ long; zoospores spherical or slightly subspherical, 3–5 μ in diameter, with a single colorless eccentric oil globule and a long flagellum, escaping upon the dehiscence of a convex terminal operculum, movement hopping; resting spore not observed.

Parasitic on *Melosira varians*, Sparrow (*loc. cit.*), UNITED STATES; Sparrow (1936a:437, pl. 15, figs. 12–14), ENGLAND.

Although the development of the sporangium of this species has not been studied, it is probably similar to that found in *Chytridium Schenkii* and *Rhizidiopsis*.

CHYTRIDIUM CURVATUM Sparrow

Amer. J. Bot., 20:69, text fig. 1n. 1933

(Figure 21 G, p. 330)

Sporangium strongly arched, broadly obpyriform or clavate, smooth-walled, 8 μ in diameter tapering to 5 μ in diameter by about 18 μ in length, with an apical operculum about 5 μ in diameter, having at the base a thick-walled, goblet-like sterile portion from which a short peglike hyaline stalk emerges, the latter not penetrating the host wall but merely attached to it; zoospores 5 μ in diameter, uniflagellate, with a single colorless oil globule, escaping upon the dehiscence of the operculum; resting spore not observed.

On *Stigeoclonium sp.* (gelatinous sheath?), UNITED STATES.

Aside from its arched habit, the organism superficially resembles *Podochytrium clavatum* Pfitzer, especially in the possession of a thin

sterile basal portion. The presence of an operculum, however, as well as the character and mode of attachment of the sporangium, sharply marks it from *Podochytrium*, as well as from other species of *Chytridium*. It is probably saprophytic on the gelatinous sheath of the alga, since no disintegration of the contents of those cells bearing sporangia was noticed.

CHYTRIDIUM EPITHEMIAE Nowakowski

Cohn, Beitr. Biol. Pflanzen, 2:82, pl. 4, figs. 12-13. 1876

Sporangium broadly subglobose, with a prominent rounded apiculus, 12μ in greatest diameter, prolonged basally into a narrow stalk which rests with its knoblike tip on the surface of the host cell, wall somewhat thickened, colorless, smooth; rhizoids not observed; zoospores not observed, probably few, emerging upon the dehiscence of a subapical convex operculum; resting spore not observed.

On *Epithemia zebra*, GERMANY.

Nowakowski regarded the apical protuberance as a second, non-functional, operculum. It is more likely an apiculus similar to that formed in *Sporophlyctis*, *Blyttiomycetes*, and several other chytrids.

The fungus on *Melosira* and *Tabellaria* doubtfully referred to this species (Sparrow, 1933a:68, fig. 1 d-f) is now considered distinct from it. See *Chytridium nodulosum*, sp. nov., below.

CHYTRIDIUM NODULOSUM, sp. nov.¹

(Figure 21 H, p. 330)

Sporangium ovoid to pyriform, $6-13 \mu$ in diameter by $10-15 \mu$ in length, with an apical operculum 5μ in diameter and a subapical rounded protuberance, resting on a short basal cylindrical stalk which is slightly expanded at its terminus, wall smooth, colorless; rhizoids not observed; zoospores probably fully formed within the sporangium, spherical, 3μ in diameter, with a centric colorless globule and a fairly long flagellum, emerging upon the dehiscence of the operculum

¹ *Chytridium nodulosum*, sp. nov.—Sporangium ovoideum vel piriforme, $6-13 \mu$ diam., $10-15 \mu$ long., bulla subapicali rotundata operculo quo 5μ diam., apicali, praeditum, stipe brevi cylindrico deorsum paulo expanso, membrana laevi, hyalina; rhizoides nondum visis; zoosporis probabiliter intra sporangium maturantibus, sphaericis, 3μ diam., globulo centrico hyalino praeditis atque cilio modice longo, simul cum dehiscencia operculi emergentibus et nondum dispersis globulum compactum formantibus ad ostiolum; sporis perdurantibus ignotis.

Species parasitica in *Melosira varianti* et *Tabellaria*, U. S. A.

and forming a compact spherical mass at the orifice before dispersing; resting spore not observed.

Parasitic on *Melosira varians*, *Tabellaria* sp., UNITED STATES.

This species was doubtfully assigned to *Chytridium Epithemiae* Nowak. in a previous publication (Sparrow, 1933a:68, text fig. 1 d-f). Since little is known of Nowakowski's fungus save from his short description and his two figures, one of an empty sporangium, the other of an undischarged one, and since the operculum in his organism was subapical, it has been thought best to segregate from it the species on *Melosira* and *Tabellaria*.

A further study of the original drawings and a few sporangia still available in a glycerin mount seems to indicate that the sporangium stalk is extramatrical rather than within the alga as previously supposed. The subapical protuberance no doubt arises from a type of development similar to that found in *Chytridium Schenkii*, where an unexpanded portion of the wall of the original zoospore persists.

CHYTRIDIUM CHAETOPHILUM Scherffel

Arch. Protistenk., 53:45, pl. 2, figs. 87-94. 1925

Sporangium sessile, short and sausage-shaped, broad-ovoid from above, 9-11 μ long by 6 μ in diameter, resting crosswise on the seta of the alga, wall thin, colorless, the upper half bearing a tuft of long solid delicate unbranched hairs; rhizoid, so far as is known, consisting of a short peglike tube which just pierces the cell wall; zoospores spherical, 2-3 μ in diameter, with a prominent eccentric colorless oil globule and a long delicate flagellum, discharged after the gelatinization of a basal part of the sporangium or by a bursting apart of the sporangium, remaining motionless for a time after discharge, movement dancing or hopping; resting spore epibiotic, sessile, nearly spherical, 5-8 μ (mostly 8 μ) in diameter, with a thick double wall the outer surface of which bears a series of regularly arranged short rodlike blunt protuberances, contents granular, with a large (5 μ) oil globule, germination not observed; male cell laterally attached, spherical, smooth, thin-walled, 2-3 μ in diameter.

On setae of *Bulbochaete* sp., Scherffel (*loc. cit.*), HUNGARY; *Oedogonium* sp., Sparrow (1933c:526, fig. I, 11-12), UNITED STATES; *Bulbochaete* sp., *Typha* pollen, Sparrow (1936a:438, pl. 15, fig. 18), substratum (?), coll. Odam, communication, ENGLAND.

The proper disposition of this species is puzzling. If, as Scherffel asserts, the zoospores are discharged after the gelatinization of a basal part of the sporangium or by a bursting apart of the sporangium, and if the resting spores are epibiotic, the species can hardly belong in *Chytridium*. Mere bursting of the wall would not seem comparable with the formation of a definite operculum. Further observations on spore discharge and the nature of the rhizoidal system (it may, indeed, be *Phlyctidium*-like) are necessary to determine the precise affinities of the fungus. *Rhizophyidium v. Mindenii* Valkanov (1931a:363) may be identical with Scherffel's organism, but since only empty sporangia without rhizoids were described, comparison of any significance is hardly possible.

No zoospore discharge was seen in any of the British or American material. The peglike endobiotic part resembles that formed by a species of *Phlyctidium*.

According to Dr. C. L. Odam (communication), the hairs of this species, found by him in England, are always bifurcated at their termini. The tips are extremely delicate and scarcely visible.

CHYTRIDIUM CONFERVAE (Wille) Minden

Kryptogamenfl. Mark Brandenburg, 5:368. 1911 (1915)

(Figure 21 J, p. 330)

Rhizidium Confervae Wille, Vidensk. Selsk. Skr. Christiana (Mat.-Nat. Kl.), 1899 (3):1, figs. 1-3.

Phlyctochytrium Confervae (Wille) Lemmerman, Abhandl. Naturwiss. Vereins Bremen, 17 (1):194. 1901.

Sporangium sessile, rarely on a short isodiametric stalk, upright or slightly tilted, broadly or narrowly ovoid, occasionally obovoid, 18-40 μ high by 15-32 μ in diameter, with a flattened apex bearing two opposite solid slightly incurved sharp teeth up to 6 μ long by 2-4 μ at base (rarely one), wall smooth, colorless; rhizoids arising as single isodiametric filaments from either side (rarely one side) of a broadly fusiform, rarely spherical, subsporangial swelling 7-15 μ in diameter by 3-6 μ high, remaining isodiametric, rarely branched, and about 2-2.5 μ in diameter save when meeting a cross wall, where they expand to 4 μ or more, strongly polyphagous, penetrating as many as forty or more cells of the alga, which they stimulate to form protective thickenings of the transverse walls; zoospores spherical, 5 μ in diameter, with a slightly eccentric colorless strongly refractive

protruding globule, flagellum 27μ long, upon the dehiscence of a slightly convex round operculum $10-12 \mu$ in diameter escaping fully formed in a compact temporarily vesiculate motionless group, suddenly assuming violent individual motion, eventually freeing their flagella and hopping away, movement intermittently amoeboid; resting spore not known with certainty.

Parasitic on *Tribonema bombycinum*, Wille (*loc. cit.*), SWEDEN; Scherffel (1925b:32, pl. 2, figs. 63-80), HUNGARY; Sparrow (1939a: 124), UNITED STATES; coll. Odam, communication and drawings, ENGLAND.

Scherffel has found two types of resting structures associated with the sporangial stage of this species, but neither can be said with certainty to belong to it. The first was epibiotic, sessile, spherical or subspherical, and $9-16 \mu$ (mostly 14μ) in diameter exclusive of the ochre-yellow episporium, which was $2-3 \mu$ thick, irregular, and covered with blunt knoblike protuberances; the endospore wall was smooth and $1.5-2 \mu$ thick, and the fatty plasma of the contents bore a single colorless globule $8-11 \mu$ in diameter. At the base was a smooth spherical or clavate empty structure which presumably functioned as a contributing cell in a sexual process. The second type of resting spore occurred singly within the horned sporangia; it was spherical and covered with a network of ridges.

Both forms have been observed in Michigan material, but neither has been convincingly connected with the sporangial stage of the species. Careful observations on the second type of spore, which, as Scherffel suggests, probably belongs to a parasitic organism, reveal minute spines in addition to the reticulations on the outer wall.

The reactions of the host to the incursions of the fungus are very marked and involve the formation of conspicuous protective plugs of cellulose on the walls wherever the vegetative system attempts entry. Scherffel has noted that, in this reaction, the nucleus of the alga is drawn away from its central position in the cell and, with a concentration of plasma, takes up a position close to the attacked cross wall. This, he asserts, lends support to the idea that the nucleus plays a rôle in wall formation. Under high magnifications it can be clearly seen that the protective plug when penetrated by the fungus is not pierced in a single place but in several. It is possible that the fungus is unwalled when passing through these plugs.

In the American material early stages in the development show

that the rhizoid is well established before the apophysis makes its appearance. Although Scherffel states that no central vacuole is formed in the sporangium during the process of maturation, it has been observed in a number of instances in the Michigan material.

CHYTRIDIUM SCHENKII (Schenk) Scherffel

Arch. Protistenk., 54:237, pl. 10, figs. 125-129, pl. 11, figs. 130-132. 1926

Rhizidium intestinum Schenk, pro parte, Ueber das Vorkommen contractiler Zellen im Pflanzenreiche, p. 5. Würzburg, 1858.

Rhizidium Schenkii Dangeard, Ann. Sci. Nat. Bot., VII, 4:297, pl. 13, figs. 24-30. 1886.

Phlyctochytrium Schenkii (Dang.) de Wildeman, Ann. Soc. Belge Micro. (Mém.), 20:48. 1896.

Sporangium variable in shape, ovoid, ellipsoid, or pyriform, 15 μ high by 10 μ in diameter, erect or procumbent, with a prominent apical papilla surmounted by a smooth convex operculum 3 μ in diameter, the colorless wall bearing a small lateral or basal colorless thick-walled hemispherical protuberance (the persistent zoospore case), otherwise thin and smooth; rhizoids branched, well developed in one or more cells of the substratum, occasionally becoming extra-matrical, arising generally from the base of an endobiotic subsporangial spherical apophysis 8-10 μ in diameter; zoospores spherical, 2-3 μ in diameter, with a colorless eccentric or centric globule and a long flagellum, emerging upon the dehiscence of the operculum and forming a motionless mass possibly surrounded by a vesicle, after a period of rest assuming motility; resting spore endobiotic, spherical, 10 μ in diameter, colorless, with a thick smooth wall and highly refractive oily contents, apparently without rhizoids, at germination forming an epibiotic sessile narrowly ellipsoidal erect or somewhat procumbent sporangium 15 μ high by 10 μ in diameter, with a smooth colorless thin wall and an apical operculum 3 μ in diameter, zoospores spherical, 2 μ in diameter, with a single globule and a flagellum 10 μ in length.

On *Oedogonium* sp., Schenk (*loc. cit.*), no specific substratum, Minden (1915:340), *Closterium* sp., Cejp (1938a:5, pl. 1, fig. 12), GERMANY; *Bulbochaete* sp., *Spirogyra* sp., *Zygnema* sp., *Closterium* sp., *Cladophora* sp., *Oedogonium* sp., Dangeard (*loc. cit.*), *Spirogyra*, de Wildeman (1894:155), FRANCE; *Oedogonium* sp., de Wildeman

(1895a:72, pl. 2, figs. 13-16), SWITZERLAND; *Oedogonium sp.*, *Cladophora sp.*, de Wildeman (1890:6, fig. 1), BELGIUM; oögonia, oöspores, vegetative cells of *Oedogonium sp.*, Scherffel (*loc. cit.*; 1914), *Oedogonium sp.*, *Spirogyra sp.*, Domján (1936:49, pl. 1, figs. 42-43, 60-61), HUNGARY; *Oedogonium sp.*, *Bulbochaete sp.*, *Spirogyra sp.*, *Closterium sp.*, Petersen (1909:416, fig. 22g; 1910:550, fig. 22g), DENMARK; *Oedogonium sp.*, Sparrow (1932b:280, fig. 3 a-d; 1933a:67, fig. 1q), UNITED STATES.

In its present form *Chytridium Schenkii* is probably a composite species made up of several varieties, some of which have been published as distinct entities. Thus *C. gibbosum* Scherffel and *C. aggregatum* Karling have been suggested by their authors to be only doubtfully distinct from it. They are, however, maintained separate in the present monograph. Some of the records of occurrence listed above are, from examination of the figures, to be accepted with reservations. It is remarkable that of the many reports of this fungus only one of the descriptions includes any measurements of the sporangium and apophysis; significant variations in the size of these structures, consequently, cannot be given.

The British fungus discussed as *Chytridium Schenkii* (Sparrow, 1936a:431) seems closer to *C. Scherffelii* Sparrow.

Scherffel first emphasized the fact (noted by Schenk) that the sporangium developed by lateral and upward expansion of a portion of the body of the infecting zoospore and that the remainder persisted as a distinct protuberance on the sporangium wall. He also pointed out that similar protuberances are found on Schenk's and Dangeard's fungi.

It is not unlikely that an inoperculate form with this type of development and similarly shaped sporangia may be found, in which event doubt will be thrown on the advisability of considering Dangeard's form (in which no operculum was observed) identical with *Chytridium Schenkii*.

CHYTRIDIUM OEDOGONII Couch

J. Elisha Mitchell Sci. Soc., 54:256, pl. 24. 1938

"Sporangia attached to the host by a nipple-like projection, the old zoospore; usually ovoid and broadest in the distal half, 10-17.6 \times 17-26 μ . Intramatrical vesicle about spherical, 10-16 μ thick,

giving rise to a long unbranched (usually) thread-like rhizoid, 1.5–2.5 μ thick. Sporangia opening by a lid. Zoospores collecting in a ball at the tip of the sporangium, 4–5.4 μ thick, uniciliate. Resting spore intramatrical, spherical or slightly flattened, 13.4–17.6 μ thick, wall about 1.2 μ thick, smooth; with a single large eccentric oil globule" (Couch, *loc. cit.*).

On *Oedogonium*, UNITED STATES.

CHYTRIDIUM KOLIANUM Domján

Folia cryptogam., 2 (1):27, pl. 1, figs. 88, 90–92, 101–106. 1936

Sporangium sessile, spherical, subspherical, or ellipsoidal, 17.5 μ in diameter by 12.5–20 μ high, wall smooth, thin, even, with the cyst of the infecting zoospore persisting as a subapical or lateral hemispherical refractive somewhat thick-walled appendage; rhizoids not well developed, branched, arising from the base of an endobiotic subsporangial somewhat ellipsoidal swelling, 10–22 μ in diameter by 12.5–25 μ high; zoospores typically chytridiaceous, 5 μ in diameter, emerging after the dehiscence of a persistent adherent operculum formed from the whole upper part of the sporangium; resting spore not observed.

Saprophytic on *Spirogyra*, *Zygnuma*, HUNGARY.

The species differs from *Chytridium Schenkii* in the shape of the sporangium and the larger operculum, from *C. gibbosum* in the shape of the sporangium and the evenness of its contour, and from *C. aggregatum* by the presumably colorless wall of the cyst.

CHYTRIDIUM AGGREGATUM Karling

Mycologia, 30:302, text figs. 1–19. 1938

(Figure 21 K, p. 330)

"Thalli numerous and gregarious, partly intra- and extramatrical, eucarpic. Zoosporangia extramatrical, formed as a lateral or slightly basal outgrowth from the encysted zoospore case and delimited from the apophysis by a cross wall at maturity; hyaline, smooth, oval, egg-shaped, subspherical, $4 \times 6 \mu$ – $10 \times 18 \mu$, with a conspicuous amber or brown protuberance, the zoospore case, near the base, and an apical or slightly sub-apical exit papilla; operculum spherical, 4–8 μ , or slightly oval. Zoospores hyaline, conspicuously uniguttulate,

spherical, 3-4.5 μ , posteriorly uniciliate; emerging in a globular mass and lying quiescent near the exit papilla for a few moments before moving apart; motility confined to a few jerky motions and amoeboid movements; settling down on the host cell and germinating in a mass in the vicinity of the zoosporangium. Apophysis intramatrical, spherical, 5-10 μ , oval, broadly spindle-shaped, elongated and occasionally constricted. Rhizoidal system well developed and branched, extending often to a distance of 110 μ ; main axis 3-4 μ in diameter. Resting spores intramatrical, hyaline, spherical, 5-14 μ , oval, slightly citriform, 6 \times 9 μ -12 \times 14 μ , somewhat depressed, and occasionally flattened or constricted, usually with a single large refractive globule and a 2.5-3 μ thick, smooth wall; germination unknown" (Karling, *loc. cit.*).

Saprophytic on *Spirogyra crassa*, *Oedogonium sp.*, and *Cladophora sp.*, Karling (*loc. cit.*), *Cladophora*, Sparrow (MICHIGAN), UNITED STATES.

Differing from *Chytridium Schenkii* only in the brown or amber zoospore case. The gregarious habit is not a constant one, and sporangia of the species have been found many times in Michigan occurring singly on algal cells.

CHYTRIDIUM GIBBOSUM Scherffel

Hedwigia, 41:(105). 1902; Arch. Protistenk., 54:239, pl. 11, figs. 133-134.
1926

Sporangium sessile, utriculate, somewhat tubular, gibbose dorsally, erect, oblique, or decumbent, thin-walled, bearing laterally at the base the thick-walled half-spherical unexpanded remnant of the zoospore case; rhizoids arising from two lateral opposite prolongations of a spherical or somewhat flattened endobiotic subsporangial apophysis; zoospores with a single globule and a flagellum, escaping upon the dehiscence of a slightly convex operculum 4 μ in diameter, movement hopping; resting spore not observed.

Saprophytic on filaments of *Cladophora fracta*, *Closterium*, HUNGARY.

Considered by Scherffel as being possibly only a subspecies of *Chytridium Schenkii*, but differing from that species in having a more tubular and gibbose sporangium. On *Closterium* the sporangia were

more ovoid than on *Cladophora*, approaching in this respect those of *C. Schenckii*.

CHYTRIDIUM SCHERFFELII (Scherffel) Sparrow

J. Linn. Soc. London (Bot.), 50:431. 1936

Chytridium pusillum Scherffel, Abstracts of Communications, V Inter. Bot. Congress, Cambridge, 1930:223; Arch. Protistenk., 73:143, pl. 9, fig. 4 a-f. 1931. Non *C. pusillum* Sorokin, Arch. Bot. Nord France, 2:24, fig. 23. 1883 (separate).

Zoosporangia broadly obovoid, with the half-spherical rounded top somewhat expanded laterally, tapering basally, mostly 6–10 μ high by 5–6 μ thick, larger specimens more oblong to obpyriform, up to 10 μ by 6 μ , with a delicate smooth colorless wall, often asymmetrical when several occur on the same host cell, the lower part being one-sidedly expanded and appearing inclined to the substratum, operculum strongly convex, usually persistent, 2–4 μ in diameter; endobiotic part a subsporangial spherical apophysis 4 μ in diameter, without rhizoids, often containing a large oil globule; zoospores emerging individually through a large apical opening, body spherical (2–3 μ in diameter), with a colorless eccentric globule and a single flagellum; resting spore not observed.

On *Characiopsis minuta* (?) (in plankton), Scherffel (*loc. cit.*), HUNGARY.

The fungus reported in *Oedogonium* from England by Sparrow (1936a:431, pl. 15, figs. 15–16) may possibly belong here. It differs in having larger sporangia and a larger apophysis provided with rhizoids; endobiotic smooth-walled resting spores were found associated with the zoosporangia.

CHYTRIDIUM INFLATUM Sparrow

Amer. J. Bot., 20:65, text fig. 1 j-l. 1933

(Figure 21 I, p. 330)

Sporangium sessile, broadly pyriform or urn-shaped, with a prominent apical papilla surmounted by a strongly convex operculum, wall smooth, colorless; endobiotic part consisting of a spherical subsporangial apophysis apparently devoid of rhizoids; zoospores fully formed within the sporangium, uniflagellate, spherical, with a single centric colorless globule, upon the dehiscence of the operculum emerg-

ing and forming a temporary group with intertwined flagella before darting away, movement hopping; resting spore not observed.

Parasitic on *Cladophora* sp., Sparrow (*loc. cit.*), UNITED STATES; *Oedogonium* sp., Sparrow (1936a:437, pl. 15, fig. 19), ENGLAND.

Two well-defined size classes were found:

1. Sporangium 15 μ in diameter by 17 μ high; apophysis 9 μ in diameter; operculum 6 μ in diameter; zoospores 5 μ in diameter, with a small globule.

2. Sporangium 7 μ in diameter by 10 μ high; apophysis 5 μ in diameter; operculum 4 μ in diameter; zoospores 3 μ in diameter, with a relatively large globule.

The species is very doubtfully separate from *Chytridium Lagenaria* Schenk, differing only in having more distinctly pyriform sporangia and a more strongly convex operculum.

CHYTRIDIUM BREVIPES Braun

Monatsber. Berlin Akad., 1856:587

Sporangium sessile, obovoid, broadly ovoid, or urceolate, 27 μ high by 20 μ in diameter, the slightly convex operculum usually terminating in a conical umbo, wall smooth, colorless; endobiotic part consisting of a thin-walled spherical subsporangial swelling without rhizoids which at maturity is cut off from the sporangium by a knoblike or conical septum; zoospores spherical, 5 μ in diameter, with an eccentric colorless globule 2 μ in diameter in the finely granular plasma and a flagellum 45 μ in length, ejected at the dehiscence of the operculum through a broad apical pore and forming a temporarily motionless mass, movement hopping or amoeboid; resting spore endobiotic, smooth-walled, with a large oil globule, germination not observed.

On oögonia of *Oedogonium flavescens*, *O. apophysatum*, Braun (*loc. cit.*), GERMANY; *Oedogonium Voucherii*, *Oedogonium* sp., Scherffel (1926a:225, pl. 10, figs. 107-109, 111-114), HUNGARY.

Considered by Fischer (1892:126) and Minden (1915:366) only a small form of *Chytridium olla*; the observations of Scherffel (*loc. cit.*) that the small size is maintained even when the fungus occurs alone on the host cell, as well as his confirmation of the fact noted by Braun (not mentioned by Fischer and Minden) that there was an

endobiotic swelling, indicate that we are dealing with a distinct species. See remarks under *C. acuminatum* Braun.

CHYTRIDIUM LAGENARIA Schenk, pro parte

Ueber das Vorkommen contractiler Zellen im Pflanzenreiche, p. 5, figs. 11-13.
Würzburg, 1858. Non *C. Lagenaria* Schenk, Verhandl. Phys.-Med.
Gesell. Würzburg, A. F., 8:241. 1858

(Figure 21 L-M, p. 330)

Rhizidium Lagenaria (Schenk) Dangeard, Le Botaniste, 1:64, pl. 3, fig. 23. 1889.

Rhizidium Westii Massee, British Fungi, p. 155, pl. 2, figs. 36-37. London, 1891.

Phlyctochytrium Westii (Massee) de Wildeman, Bull. Soc. Roy. Bot. Belg. (Mém.), 35:48. 1896.

Sporangium sessile, spherical, subspherical, ovoid, urceolate, or broadly pyriform, somewhat dome-shaped when immature, variable in size, wall somewhat thickened, smooth, colorless; rhizoids generally stout, up to 9 μ in diameter at the point of origin, much branched, occasionally absent, when present usually arising from a single axis produced at the base of a spherical, subspherical, flattened, fusiform, or broad tubular apophysis of variable size; zoospores spherical or somewhat ovoid, 3-5.5 μ in diameter, with a colorless centric or eccentric globule and a flagellum about 20 μ in length, emerging through a large apical pore formed upon the dehiscence of a convex smooth operculum and collecting at the orifice in a temporarily motionless mass, movement swimming or amoeboid; resting spore spherical or ovoid, 18-30 μ in diameter, with a smooth colorless wall 2-3 μ thick, the contents with a single large colorless globule, rhizoidal system like that of the sporangium, upon germination forming an epibiotic sessile ovoid, subspherical, somewhat flattened, or pyriform operculate sporangium.

On *Nitella flexilis*, Schenk (*loc. cit.*), GERMANY; *Vaucheria* sp., Dangeard (1889b:64, pl. 3, fig. 23), FRANCE; *Spirogyra* sp., *Cladophora* sp. (?), de Wildeman (1890:14, fig. 4), BELGIUM (?); *Oedogonium* sp. (?), Constantineanu (1901:383), RUMANIA; *Spirogyra* sp., *Cladophora* sp., Massee (1891:155, pl. 2, figs. 36-37), *Rhizoclonium hieroglyphicum*, Sparrow (1936a:432, pl. 16, figs. 1-24), ENGLAND; *Oedogonium* sp., Karling (1936a:619, figs. 1-2), *Cladophora* sp., Sparrow, UNITED STATES.

The records of de Wildeman and Constantineanu are open to question, since no operculum was seen. Their fungi may in reality be *Phlyctochytrium Lagenaria* (Schenk) Domján. *Rhizidium Westii* Massee is considered doubtfully synonymous with the present species. It resembles in all essentials *Chytridium Lagenaria* except that no operculum was observed. This may have been overlooked by Massee. If not, Massee's fungus still cannot, because of differences in the shape of the sporangium and the stoutness of the rhizoidal system, be referred to *P. Lagenaria*.

Chytridium Lagenaria has been the object of rather intensive investigation (Sparrow, *loc. cit.*; Karling, *loc. cit.*), and a relatively large amount of data has been accumulated on its development and biology.

The fungus was transferred from *Rhizoclonium* to *Spirogyra* sp. and *Oedogonium* sp. to determine any morphological changes which might occur on these substrata (Sparrow, *loc. cit.*). It was found, under the conditions of the experiments (conducted in van Tieghem cells), that (1) the size and nature of the zoospore remained constant on the three algae; (2) an endobiotic apophysis was always formed and, though varying in size (average variation from 9–23 μ), was never larger than the operculate sporangium; (3) the sporangium maintained the same general shape (usually subspherical) at all times, but exhibited striking variations in size when growing on different algae. On *Rhizoclonium* the sporangia averaged 29 μ (limits of variation 20–35 μ); on *Spirogyra*, 8 μ (6–11 μ); and on *Oedogonium*, 13 μ (12–15 μ). These variations were not necessarily coöordinated with differences in the diameter of the algal cell, for though the largest sporangia were formed on the alga having the largest cells (*Rhizoclonium*) the smallest were not formed on the most slender filaments (*Oedogonium*), but on *Spirogyra*. The rhizoidal system also underwent marked variation on the three algae, being extremely stout and well developed in *Rhizoclonium*, very sparse in *Spirogyra*, and either so tenuous as to be invisible or entirely lacking in *Oedogonium*. Karling has grown the fungus on a variety of Conjugatae and other green algae as well as on *Chara* and *Nitella*, all of which had previously been killed by boiling. No quantitative or qualitative data are given for the fungus on these different substrata. The success of Karling's efforts to cultivate it saprophytically makes him inclined to doubt that the species is at all parasitic and to question

the validity of the cross-inoculation experiments mentioned above so far as they indicate actual parasitism of the three hosts. The purpose of these experiments was not primarily to test the range of parasitism, but rather to observe morphological changes in the fungus when it was growing on different algae. It might be emphasized, however, that while the environment of a van Tieghem cell is not a natural one, it is not necessarily unfavorable, and that in both controls and infected cells the algae not only appeared healthy, save where attacked by the zoospores of the fungus, but showed evidences of cell division and growth. The demonstration of saprophytism is direct and certain; it is not, however, evidence which necessarily disproves a fact noted in many other fungi, namely, that they may at times also attack a viable organism.

From these researches it is certain, at any rate, that the species can exist on a fairly wide variety of substrata, and in view of this circumstance it is surprising that it has not been recorded more often. Such studies as have been made on *Chytridium Lagenaria*, especially those dealing with qualitative and quantitative changes occurring in the fungus on different substrata, will eventually have to be made for all species of the order, before a really comprehensive taxonomic treatise can be prepared.

A curious conjugation of encysted zoospores with young thalli developing in pure water was observed (Sparrow, *loc. cit.*). After the contents of the quiescent spore had evacuated the cyst and had flowed into the receptive thallus, the latter underwent a remarkable vegetative development, which in some cases appeared to terminate in the production of a dwarf sporangium. The result of this fusion was not the formation of a resting structure, as might be expected, but the rejuvenation of vegetative growth and the prolongation of the life of the organism. These thalli continued their growth for nearly a week and became very extensive in contrast to ordinary germinating zoospores, which under the same conditions disintegrated within twelve hours.

Both Sparrow and Karling have observed the apparently asexually formed resting spores, which, as the latter investigator points out, are merely enlarged and encysted apophyses. Karling also observed their germination, in which process the resting spore functioned as a prosporangium.

CHYTRIDIUM CODICOLA Zeller

Publ. Puget Sound Biol. Station, 2:121, pl. 20, figs. 5-7. 1918

Sporangium erect, sessile, globose to ovoid, 20-34 μ in diameter, wall smooth, colorless; rhizoid broad, often swollen or vesiculate, or consisting of two lobelike saccate branches; zoospores spherical, 3-4 μ in diameter, with a single refractive colorless globule and a long flagellum, escaping through an apical or slightly subapical circular exit pore 6-8 μ in diameter formed upon the dehiscence of an operculum which does not interrupt the even contour of the sporangium; resting spore not observed. (Modified from Zeller.)

On *Codium mucronatum*, UNITED STATES (Pacific coast).

CHYTRIDIUM POLYSIPHONIAE Cohn

Hedwigia, 4:169. 1865; Schultze, Archiv mikro. Anat., 3:40, pl. 2, fig. 2. 1867

(Figure 21 N-P, p. 330)

Rhizophyidium Polysiphoniae (Cohn) H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):486, fig. XI, 5-8.

Rhizophyidium olla H. E. Petersen, op. cit., p. 485, fig. XI, 4.

Sporangium sessile, subspherical, subangular, pyriform, or urceolate, 12-33 μ in diameter by 12-42 μ high, resting with its broad base on the substratum, wall fairly stout, colorless, yellowish, or dark, not of cellulose, smooth or densely punctate; rhizoids unbranched or branched; zoospores spherical, 2.5-4 μ in diameter, with a colorless centric or eccentric globule and a fairly long flagellum, escaping upon the dehiscence of an apical smooth convex operculum 7-13 μ in diameter; resting spore not observed.

On *Polysiphonia violacea*, Cohn (loc. cit.), GERMANY; *Polysiphonia violacea*, P. *urceolata* (coll. Rosenvinge), Petersen (loc. cit.), *Ceramium rubrum*, *Ceramium* sp. (coll. Rosenvinge), Petersen (loc. cit.), *C. strictum*, Petersen (loc. cit., p. 488, "no. 5"), *Delessaria sanguinea*, *Callithamnion* sp., Petersen (loc. cit.), *Ceramium fruticulosum*, Sparrow (1934c:23, pl. 4, figs. E-G), DENMARK; *Pylaiella littoralis* (coll. Rosenvinge), Petersen (loc. cit.), GREENLAND; *Polysiphonia fibrillosa*, *Ceramium rubrum*, Sparrow (1936b:255, text fig. 31), UNITED STATES.

The species as described here is undoubtedly a composite one and much work will be needed to separate the varieties or even the species which it now embraces.

Cohn's fungus had irregularly pyriform sporangia, 25-33 μ in diameter, which rested with their broad bases on the alga. The wall was somewhat thickened, dark, and punctate, and no rhizoids were observed. At maturity an operculum 13 μ in diameter was dehisced from the protruding apex, allowing the zoospores, 2.5 μ in diameter, to escape. Petersen's specimens differed in having the operculum slightly subapical and the sporangium wall colorless and smooth; an unbranched rhizoid was observed. He (*op. cit.*, p. 487) suggests that the coloration and punctuation of the sporangium wall described by Cohn were probably caused by age. Sparrow's Danish material differed from Cohn's chiefly in having a smaller operculum (7 μ in diameter), larger zoospores (4 μ in diameter), and a smooth colorless sporangium wall, and from Petersen's in having an apical operculum and rhizoids, which were probably branched, arising from a central stalk.

Rhizophyidium olla Petersen on *Pylaiella* from Greenland cannot be distinguished morphologically from *R. Polysiphoniae* on the basis of the description and figures given. Cohn has called attention to the fact that his fungus was confounded with the spermatia of *Nitophyllum* by Derbés and Solier. Other instances of early investigators' confusing the fungus with an organ of the alga are given by Wright (1879b).

CHYTRIDIUM MEGASTOMUM Sparrow

Dansk Bot. Ark., 8(6):21, pl. 4, A-D. 1934

(Figure 21 Q, p. 330)

Sporangium sessile, obpyriform, 12-18 μ high, diameter at the base 5-7 μ , increasing distally to 10-15 μ at the apex, wall smooth, colorless; rhizoids rudimentary, sparingly branched, arising from a single stalk; zoospores spherical, 3 μ in diameter, with a small colorless slightly eccentric globule, discharged through a broad usually somewhat subapical pore 8-10 μ in diameter formed upon the dehiscence of a large convex operculum; resting spore not observed.

Parasitic on the setae of *Striaria attenuata*, Sparrow (*loc. cit.*), DENMARK; *Ceramium diaphanum*, Sparrow (1936b:255), UNITED STATES.

Distinguished from its closest marine relative, *Chytridium Polysiphoniae*, by the obpyriform shape of its sporangium and the subapical operculum.

IMPERFECTLY KNOWN SPECIES OF CHYTRIDIUM

? CHYTRIDIUM CHARACII Scherffel

Arch. Protistenk., 53:13, pl. 1, fig. 25 a-c. 1925

Sporangium and zoospores not observed; resting spore epibiotic, narrowly ovoid, oblong, or somewhat clavate, with the long axis perpendicular to the substratum, $5-6 \mu$ in diameter by $10-14 \mu$ high (smaller examples $4-7 \times 7-9 \mu$), colorless, with an extremely thick wall of two layers, the inner thick, refractive, homogeneous, and smooth, the outer thicker at base or apex than in the mid-region, in optical section having a well-defined prismatic structure, in surface view covered by longitudinal rows of elongate warts, with a delicate branched rhizoid within the host, germination not observed; companion cell spherical or somewhat clavate, thin-walled, $2-2.5 \mu$ in diameter, sessile, without rhizoids, connected to the base of the resting spore by a more or less elongate narrow fertilization tube.

Parasitic on *Characium sp.*, HUNGARY.

Observations on the sporangial stage will be necessary before this fungus can be placed in the correct genus. Scherffel has suggested that it may belong possibly in either *Zygorhizidium* or *Rhizophydium*.

? CHYTRIDIUM CHLAMIDOCOCCI Braun

Abhandl. Berlin Akad., 1855:45. 1856

Sporangia in groups, at first spherical, later somewhat oblong, not over 10μ long, sometimes with an oblique apiculus.

On *Chlamidococcus pluvialis*, GERMANY.

Mentioned by Fischer and Minden under *Rhizophydium acuiforme* (Zopf) Fischer.

? CHYTRIDIUM CORNUTUM Braun

Abhandl. Berlin Akad., 1855:50, pl. 4, figs. 8-19. 1856

Rhizophydiwm cornutum (Braun) Rabenhorst, Flora Europaea algarum, 3:281. 1868.

Phlyctidium cornutum (Braun) Sorokin, Arch. Bot. Nord France, 2:19, fig. 14. 1883 (separate).

Sporangium sessile, at first spherical, later ellipsoidal with several hornlike outgrowths of different lengths, $10-12.5 \mu$ in diameter (without protrusions); zoospores posteriorly uniflagellate; rhizoids and resting spore not observed.

On *Anabaena circinalis*, Braun (*loc. cit.*), GERMANY; *Hormidium varium*, Sorokin (1874b:8, pl. 1, figs. 18-28; 1883:19, fig. 14), EUROPEAN RUSSIA (southern part).

Sorokin (*loc. cit.*) states that the posteriorly uniflagellate ellipsoidal zoospores escape through a pore on the upper face of the sporangium. No endobiotic part has been observed, nor has the method of opening of the sporangium been described. The fungus may possibly belong in *Rhizophydiwm*.

? CHYTRIDIUM DEPRESSUM Braun

Monatsber. Berlin Akad., 1855:383; Abhandl. Berlin Akad., 1855:46, pl. 4, fig. 7. 1856

Sporangium very broadly pyriform, resting with its wide base on the host cell, somewhat flattened, with a prolonged erect or slightly bent apiculus, wall smooth, colorless, 37μ broad by 25μ high; rhizoids, method of discharge of zoospores, and resting spore not observed.

On *Coleochaete prostrata*, coll. Pringsheim, GERMANY.

? CHYTRIDIUM ELODEAE Dangeard

Le Botaniste, 1:61, pl. 3, fig. 25. 1889

Sporangium sessile (?), nearly spherical, variable in size, up to 30μ in diameter, wall smooth, colorless; rhizoids not clearly seen; zoospores spherical, 3μ in diameter, with a prominent colorless basal globule and a fairly long flagellum, emerging from a point on the sporangium and forming a large mass from which they slowly escape.

On the cortical cells of *Anacharis canadensis*, FRANCE.

As suggested by Dangeard, this is probably an incompletely observed species of *Cladochytrium*. It should be noted, however, that the sporangia are said to be "sur les cellules" rather than inside.

? CHYTRIDIUM EUGLENAE Braun

Monatsber. Berlin Akad., 1855:382; Abhandl. Berlin Akad., 1855:47, pl. 4, figs. 26-27. 1856

Phlyctidium Euglenae (Braun) Sorokin, Arch. Bot. Nord France, 2:20, fig. 16. 1883 (separate).

Sporangium inoperculate, extramatrical, somewhat irregularly tubular, with a small knoblike sterile continuous basal or lateral part resting on the host cell, 50-66 μ long by 16-33 μ in diameter; endobiotic part not observed; zoospores ovoid, longer than wide, 3.3 μ long, with a basal colorless globule and a smaller anterior vacuole, flagellum about three times the length of the body, escaping through a pore formed at the tip of the sporangium; resting spore not observed.

Parasitic on resting cells of *Euglena viridis* (coll. von Siebold and Meissner), Braun (*loc. cit.*), GERMANY; encysted *Euglena*, Sorokin (*loc. cit.*; 1874b:7, pl. 1, figs. 12-17), RUSSIA.

Because of the lack of information on the vegetative system the species cannot be placed generically with certainty. Fischer and Minden have referred it to *Polyphagus Euglenae*, but this course seems hardly justified from the differences in shape of the sporangium, the formation of zoospores in the sporangium, and the bulbous base and colorless globule of the zoospore. On the other hand, the fungi collected by Bail and Gross and later mentioned by Braun (*loc. cit.*) in his discussion of this species are probably referable to Nowakowski's *Polyphagus*. Braun (1856b:592) subsequently referred Bail's fungus to *Rhizidium*.

Rhizidium (= *Phlyctochytrium*) *Euglenae* of Dangeard (1889b:64) approaches closely the fungus found by von Siebold and Meissner.

? CHYTRIDIUM HAEMATOCOCCI Braun

Abhandl. Berlin Akad., 1855:45. 1856

Known only from the figure of Vogt, in Desor (1844:215-219, pl. 1, figs. 4 a-f) (see Braun, 1856a).

On *Haematococcus*, SWITZERLAND (?).

Mentioned by Fischer and Minden under *Rhizophydium acuiforme* (Zopf) Fischer.

? *CHYTRIDIUM MINUS* Lacoste and Suringar

Nederl. Kruidk. Arch., 5 (2):275, pl. A. 1861

Sporangium subglobose or short-oblong, 11-14 μ high by 9-12 μ in diameter, with a broad prominent apical papilla 1.3-2.5 μ high by 2.5-4 μ in diameter, wall smooth, golden, thin in the upper part but becoming thicker toward the base, where it is prolonged into a single slender extramatrical stalk (rarely two opposite stalks) which may encircle the substratum; zoospores, method of escape, and resting spore unknown.

On *Ulothrix albicans* (?), "Conferva rhynophila," *Oedogonium* sp., *Bulbochaete setigera* (on the setae), stipes of *Gomphonema navicella*, HOLLAND.

Tokunaga (1934b:392, pl. 11, fig. 13) has referred to this species a fungus found by him in Japan on oögonia of *Oedogonium* sp. It is characterized as follows: "Zoosporangia epibiotic on sexual cells of the host, solitary or aggregated, spherical or ovoidal, 12-14.4 μ in diameter, with smooth membrane, an apical papilla and a broad, short rhizoid; zoospores globular, about 2-4 μ in diameter, with a single cilium; resting spores endobiotic, up to seven in a host cell, spherical, 13.2-15.6 μ in diameter, with smooth, thick membrane and a large oil drop." The very different nature of the rhizoid as well as the shape of the sporangium of the Japanese fungus makes it extremely doubtful that it is identical with Lacoste's and Suringar's species. Further, since an operculum has not been described as being present in either form, the placing of them in *Chytridium* seems hardly justified. The broad tubular rhizoid and the endobiotic resting spores of Tokunaga's fungus make it appear closer to *C. olla*. Sporangia exactly like those figured by Lacoste and Suringar have been found in Michigan on *Mougeotia*. In none of the numerous specimens was the rhizoid ever observed to penetrate the algal cell. Indeed, the whole aspect of the organism was animal-like rather than fungoid in character.

? CHYTRIDIUM MURICATUM Scherffel

Arch. Protistenk., 54:216, pl. 10, fig. 89. 1926

Sporangium sessile, between spines of the host, broadly ovoid, with a rounded base, somewhat higher than broad ($15 \times 12 \mu$), thick-walled, the outer surface fairly densely beset with scattered moderately thick conical spines 3μ long; with a sharply defined smooth broad apical opening which probably resulted from the dehiscence of an operculum; other characters unknown.

On the zygote of *Staurastrum dejectum* var. *Debaryanum*, HUNGARY.

This incompletely known form is interesting because of the sculpturing of the wall, in which character it resembles *Rhizophydiwm verrucosum*. It is not clear, however, whether the structure described is a sporangium or a germinated resting spore. Rhizoids and an operculum were probably formed, but were not observed.

? CHYTRIDIUM PEDICELLATUM de Wildeman

C. R. Soc. Roy. Bot. Belg. (Bull.), 30:170, fig. 1. 1891

Sporangium shaped like that of *Rhizophydiwm mammillatum*; endobiotic part consisting of a small knob; otherwise unknown.

Substratum (?), BELGIUM (?).

Possibly belonging in *Phlyctidium*.

? CHYTRIDIUM SPIROTAENIAE Scherffel

Arch. Protistenk., 53:14, pl. 1, figs. 26-29. 1925

Sporangium sessile, broadly ovoid, its longer axis parallel with that of the host cell, $12-14 \mu$ in diameter by $8-9 \mu$ high, with a conical protuberance (papilla) eccentrically placed on the somewhat flattened upper surface, wall smooth, thin, colorless; rhizoids not observed; opening with an apical or lateral pore; resting spore extramatrical, sessile (?), colorless, spherical, $11-20 \mu$ (generally 16μ) in diameter, wall of two layers, the outer densely covered with broad, blunt or pointed, straight or slightly curved, solid, refractive, ray-like protuberances 3μ wide at the base by $2-3 \mu$ high, inner wall smooth, 2μ thick, contents colorless, with numerous coarse globules (fat?), germination not observed; male cell extramatrical, sessile

(always?), rounded, smooth, thin-walled, apparently without rhizoids, connected to the resting spore by a cylindrical tube 2μ in diameter which is expanded distally to form a spherical or pyriform swelling, the tubular part sometimes lacking.

Parasitic on *Spirotaenia condensata*, HUNGARY.

Because of the lack of data on the type of discharge of the sporangium the fungus cannot be placed generically and has hence been described under both *Rhizophydium* (p. 216) and *Chytridium*.

? *CHYTRIDIUM VOLVOCINUM* Braun

Monatsber. Berlin Akad., 1856:588

Rhizophydium volvocinum (Braun) Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4): 104. 1892.

Sporangium pyriform or flasklike, resting on a short narrow base; apparently without rhizoids; zoospores and resting spore not observed.

On *Volvox globator*, coll. Cohn, GERMANY.

Described in Fischer as *Rhizophydium (Phlyctidium) volvocinum* and in Minden as *R. volvocinum* (Braun) Fischer.

? *CHYTRIDIUM XYLOPHILUM* Cornu

Ann. Sci. Nat. Bot., V, 15:116. 1872

Rhizidium xylophilum (Cornu) Dangeard, Le Botaniste, 1:64. 1889.

Rhizophydium xylophilum (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1 (4):98. 1892.

Sporangia resting on the surface of the fibers, often in long rows, ovoid, acuminate, flattened, with or without a long tube which terminates in a papilla; rhizoids not observed; zoospores spherical, with an eccentric globule and a single flagellum, method of escape not described; resting spore free (?), spherical, with a moderately thick smooth wall and a large pale-brown oil globule.

Saprophytic on submerged decaying fibers of *Corylus avellana*, *Tilia*, hemp, FRANCE.

Both Dangeard (1886a:300, pl. 13, figs. 6-9) and Scherffel (1926a:247, pl. 11, figs. 144-146) have referred fungi which they

have found to Cornu's incompletely known species. Dangeard's chytrid rested on "fibres" and had an ovoid sporangium with a prominent apical papilla. Sporangia were also found within the tissue, where they underwent deformation. Since the zoospores upon germination in water produced rhizoids they were probably present on the natural substratum, though unobserved. Discharge presumably was inoperculate, the zoospores clustering in a rounded motionless mass from which they soon escaped. Scherffel's fungus formed sporangia on the fibers of decayed *Typha* or in the cells. When free they assumed an irregular broadly pyriform shape, generally with a somewhat laterally placed prominent papilla bearing an operculum. Others were spheroidal with a slightly elevated papilla, or broadly ovoid with a somewhat lateral tapering discharge tube. They varied in size, being 20–36 μ in diameter by 16–34 μ high. The zoospores were spherical, 8 μ in diameter. No rhizoids were observed. Scherffel's fungus differed from both Cornu's and Dangeard's in having operculate sporangia. All these fungi have been incompletely observed, and since the rhizoidal system of Cornu's plant was not found it seems useless to attempt an interpretation of his species.

Sparrow (1936a:432, pl. 15, figs. 21–26) has described an operculate fungus with pyriform or irregular sporangia imbedded in the spongy woody tissue of submerged *Aesculus* and *Quercus* twigs in England and in *Betula* in New Hampshire. Here again, however, because of the difficulty of freeing the plants intact from their substratum no complete picture of the vegetative system was obtained. From what was learned, however, this system was filamentous, hyphal, and at least occasionally septate. The sporangia were 17–45 μ in diameter by 20–45 μ high, were ordinarily provided with a broad somewhat attenuated discharge tube, and terminated in a smoothly convex or umboonate operculum. The zoospores were posteriorly uniflagellate, with a single globule, and 5–7 μ in diameter. The form resembles a species of *Endochytrium* in being within the cells of the substratum, and *Chytridium xylophilum* in the general shape of the sporangia and the habitat, but if the septate hyphal characters of the mycelium are confirmed by subsequent investigation it probably represents the type of a new genus.

? CHYTRIDIUM SP., Schulz

Schriften f. Süßwasser und Meereskunde, 2(11):181, fig. 14. 1923

Sporangium sessile, spherical, 12–14 μ in diameter, wall thin, the outer surface with a minute spiral crisscross pattern, with two subapical convex opercula; rhizoid tubular, unbranched; zoospore discharge not observed; resting spore not observed.

On zygote of a desmid, GERMANY.

If the opercula described are not in reality protruding papillae the form is apparently a new species. Observations on zoospore discharge, however, will have to be made before this can be said with certainty.

EXCLUDED SPECIES OF CHYTRIDIUM

* CHYTRIDIUM ALARIUM Kibbe

Publ. Puget Sound Biol. Station, 1:221. 1916

Cystidia of the alga *Alarium*. Not a fungus.

* CHYTRIDIUM DENTRITICUM Fuckel

Fuckel Herb. No. 1608. 1894

Specimen not examined—doubtless not identifiable if dried.

* CHYTRIDIUM DESTRUENS Nowakowski

Cohn, Beitr. Biol. Pflanzen, 2(1):75, pl. 4, figs. 1 a-c. 1876

This organism is *Minutularia destruens* Dangeard (1890-91c:241), a monad.

Because of ingestion of solid particles the species is considered by Dangeard to be a protozoan, in the zoosporic monads.

* CHYTRIDIUM MESOCARPI (Fisch) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):126. 1892

Euchytridium Mesocarpi Fisch, Sitzungsber. Phys.-Med. Soc. Erlangen, 16:101. 1884.

Sporangium epibiotic, flasklike, resting on the broad base, the upper part prolonged into a short tube, with a brownish stout smooth wall; rhizoid delicate, extending to the middle of the host cell, rarely

branched; zoospores somewhat large, with the fine granular plasma containing an oil droplet, not over eight formed in a sporangium, with a single anterior flagellum attached to the somewhat narrower forward end of the body, emerging suddenly from the tip of the sporangium after the dehiscence of a circular operculum, after a period of swarming coming together in pairs and fusing at the flagella-bearing poles; the zygote containing two oil globules which fuse into one, its motion slow, soon coming to rest on the surface of the host and penetrating it by means of a small outgrowth, through which the content of the zygote is discharged into the host, where it enlarges, eventually surrounds itself with a double wall, and becomes a resting spore; the resting spore germinating after a short period, producing zoospores which penetrate other host cells and form new sporangia.

On *Mougeotia* sp., GERMANY.

Fisch says all the zoospores from the sporangia fused and unconjugated ones never formed new sporangia, as they did in *Reessia*. If this is so then only zoospores from germinated resting spores can form new sporangia (gametangia). It should be noted that the zoospores are *anteriorly* uniflagellate, a point not mentioned by Fischer and Minden, who, on the basis of Zopf's observations on *Rhizophyodium pollinis-pini*, doubt their conjugation. The lack of figures greatly weakens Fisch's account. He does not state whether an epi- or endobiotic sporangium is formed at the germination of the resting spore.

If the fungus is found again and the observations of Fisch confirmed it should be placed, on the basis of the flagellation of the zoospores and the apparent lack of true sporangia, in a new genus of the Hypocrechytriaceae.

A form mentioned by Cornu (1872a:121) "near *Chyt. acuminatum*" which has an operculate sporangium and an endobiotic spherical smooth-walled resting spore with a single globule, and which is parasitic on zygospores of *Mougeotia scalaris* in France, has been referred tentatively to this species by Fischer and Minden, apparently on the basis of the similarity of hosts.

* CHYTRIDIUM MINIMUM Braun

Monatsber. Berlin Akad., 1855:381

The antheridial cell of *Coleochaete pulvinata*, according to Pringsheim (in Braun, 1856a:34).

* CHYTRIDIUM OBLONGUM Braun

Monatsber. Berlin Akad., 1855:380

The dwarf male plant of *Oedogonium vesicatum*, according to de Bary (in Braun, 1856b:587).

CATENOCHYTRIDIUM BERDAN

Amer. J. Bot., 26:460. 1939

(Figure 22A, p. 367)

"Thallus intra- and extramatrical, predominantly monocentric, eucarpic. Zoosporangium extramatrical, operculate, delimited by a cross wall at maturity. Development of zoosporangium endo-exogenous. Apophysis intramatrical, compound, consisting of linear series of constricted, catenulate segments subtended by an extensive, richly branched rhizoidal system. Zoospores posteriorly uniciliate, emerging in a globular mass and lying quiescent for a few moments before swimming away; method of swimming rapid and darting. Resting spore extramatrical, usually formed in the same position as the zoosporangium, a segment of apophysis sometimes encysting and becoming a resting spore; germination unknown" (Berdan, *loc. cit.*).

A monotypic genus saprophytic on vegetable debris.

Distinguished from *Chytridium* by the catenulate secondary apophyses.

CATENOCHYTRIDIUM CAROLINIANUM Berdan

Amer. J. Bot., 26:461, fig. 1. 1939¹

"Zoosporangia hyaline, spherical, sub-spherical, pyriform, obovoid, ovoid, elliptical, kidney-shaped or convoluted with pointed lobes, 8-40 × 8-75 μ . Operculum apical to sub-apical in position, hinged to and persistent on the empty sporangium; orifice circular, 6-20 μ in diameter. Catenulate segments of apophysis 2-30 in number, arranged in 1-4 linear series attached to the primary apophysate cell; primary apophysate cell commonly spherical to ovoid, 5.5-22 μ ; other segments of apophysis spherical, ovoid, elliptical or irregularly elongate, joined by protoplasmic connection through the wall or by

¹ See also Berdan, Amer. J. Bot., 28:901. 1942.

an elongated isthmus. Rhizoidal system (including apophysis) 55–800 μ in extent; rhizoids from .5–3 μ in diameter, becoming very finely branched; branching somewhat dichotomous. Zoospores hyaline, spherical, 5–6 μ , uninucleate, with a single highly refractive globule about 2.5 μ in diameter; cilium 35–40 μ in length. Infecting zoospores commonly attached laterally to wall of host cell. Old zoospore case usually persistent on the zoosporangium or resting spore, flattened, hyaline or amber and thick-walled, about 8 μ in diameter. Treatment with chlor-iodide of zinc producing a pale mauve color in the sporangium wall, a deep mauve in the old spore case, a deep pinkish-mauve in the segments of the apophysis, magenta in the primary apophysate cell, barely affecting the rhizoids. Resting spore smooth, spherical to ovoid, 8–40 μ , thick-walled, light to dark brown, with one large globule and a parietal layer of smaller ones; germination unknown" (Berdan, *loc. cit.*).

Saprophytic in leaves of wheat, corn, rye, oats, and various grasses,
UNITED STATES, CANADA.

SUBFAM. ZYGORHIZIDIOIDEAE

Sporangium epibiotic, sessile, rhizoids endobiotic, delicate, and tubular or rhizoidal; resting spore epibiotic, sessile, formed after aplanogametic heterogamous sexual reproduction.

ZYGORHIZIDIUM LÖWENTHAL

Arch. Protistenk., 5:228. 1905

(Figure 2 P–Q, p. 46; Figure 21 R, p. 330)

Ectochytridium Scherffel, Arch. Protistenk., 53:7. 1925

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming either the rudiment of the sporangium or a receptive or a contributing thallus; sporangium operculate, epibiotic, sessile, formed from the enlarged body of the encysted zoospore; zoospores posteriorly uniflagellate; rhizoidal system endobiotic, consisting of a subsporangial apophysis and usually provided with an unbranched or branched broad rhizoid; resting spore epibiotic, sessile, thick-walled, formed from the body of the receptive thallus after conjugation with a smaller contributing thallus by means of a conjugation tube produced by the smaller plant, germination not observed.

A monotypic genus, known only as a parasite of Conjugatae.

Scherffel (*loc. cit.*) has proposed the name *Ectochytridium* for this genus, as a subgenus of *Chytridium*, but has used the name in a generic sense ("*E. Willei* (Löwenthal) Scherff.").

ZYGORHIZIDIUM WILLEI Löwenthal

Arch. Protistenk., 5:228, pl. 8, figs. 8-43. 1905

Ectochytridium Willei (Löwenthal) Scherffel, Arch. Protistenk., 53:7, pl. 1, figs. 11-24. 1925.

Sporangium sessile, single or in groups, spherical, subspherical, or broadly or narrowly pyriform, with a single apical, subapical, or lateral broad operculum (rarely two), wall smooth, stout, colorless, somewhat refractive, not giving a cellulose reaction, typically about 15μ in diameter, dwarf sporangia $4-5.4 \mu$ in diameter; endobiotic system consisting of a knoblike centrally depressed or irregular structure $1-2 \mu$ in diameter, from the center of which one or two tenuous generally feebly developed branched rhizoids emerge; zoospores from four to forty in a sporangium, asymmetrically ovoid, sharply acuminate posteriorly, with a single anterior colorless refractive globule and a long flagellum, emerging after the dehiscence of the strongly convex operculum, movement hopping; "male" thallus (dwarf sporangia?) pyriform, $4-5.4 \mu$ in diameter, the expanded endobiotic part with or without rhizoids, copulation tube basal or lateral, usually one (rarely two), up to 45μ long by $1-2 \mu$ in diameter, refractive, with a narrow lumen, making contact with the lower half of the receptive thallus, if not conjugating functioning as a sporangium; receptive thallus large, spherical or subspherical, the knoblike endobiotic part with or without rhizoids, after conjugation forming a subspherical resting spore $8-11 \mu$ in diameter by $7-10 \mu$ high, with a thick smooth colorless or brownish wall, contents with numerous large refractive often centrally disposed globules, germination not observed.

On *Cylindrocystis Brebissonii*, possibly only saprophytic, Löwenthal (*loc. cit.*), NORWAY; *Mougeotia parvula*, *Mougeotia sp.*, Scherffel (*loc. cit.*), *Spirogyra longata*, *Mougeotia spp.*, *Zygnuma sp.*, Domján (1936:51, pl. 1, figs. 128-129, 138), HUNGARY.

The nonsexual thalli observed by Scherffel on *Mougeotia* differed from those on *Cylindrocystis* in that they lacked an endobiotic knob and formed instead a group of very short rodlike rhizoids. They

also differed in that they caused a marked bending of the long host cell and stimulated it to form a protective plug of wall material. It is possible that this reaction of the host may account for the absence of the characteristic knob.

Scherffel's contention that the fungus called *Rhizophyllum sphærocarpum* Zopf by Atkinson (1909a) was *Zygorhizidium* is open to question. Atkinson's fungus formed sporangia of two sizes, which opened apically or laterally, and though the large ones caused bending of the *Mougeotia* cell, the small ones did not. Furthermore, extensive germ tubes were sometimes formed which ran along the outer wall of the host (interpreted by Scherffel as a conjugation tube). All these features are found in *Zygorhizidium*. But discharge of the sporangium was inoperculate, and the rhizoid on both large and small forms was, according to the figures, a single unbranched outgrowth (described, however, in the text as "consisting of a few very short branches . . .").

Zygorhizidium was also investigated cytologically by Löwenthal. He found the young thallus to be uninucleate at first and the cytoplasm strongly alveolate. As the plant increases in size the plasma becomes denser and the spherical (0.5–0.1 μ in diameter) generally homogeneous nuclei are more numerous as well as smaller and less distinct. Mitotic figures are obscure and observed with difficulty. Around each of the nuclei a portion of the protoplasm is cleaved out and the resultant zoospores are uninucleate, the nucleus lying posterior to the oil droplet. (See also under "Sexual Reproduction," p. 53.)

SUBFAM. MACROCHYTRIOIDEAE

Sporangium epibiotic, sessile, formed as a lateral walled-off outgrowth of the cylindrical main axis; rhizoids endobiotic, extensive, broadly tubular, wide-lumened, the whole plant very large; resting spore borne like the sporangium.

MACROCHYTRIUM MINDEN

Centralbl. f. Bakteriol., Parasitenk. u. Infektionskrankh., Abt 2, 8:824.

1902; Kryptogamenfl. Mark Brandenburg, 5:385. 1911 (1915);

Falck, Mykolog. Untersuch. Berichte, 2 (2): 249. 1916

(Figure 22 B-D, p. 367)

Thallus epi- and endobiotic, monocentric, euclastic, the epibiotic part forming subapically the rudiment of the sporangium or the rest-

ing spore, the endobiotic giving rise to a system of broad wide-lumened branched rhizoids; sporangium operculate; zoospores posteriorly uniflagellate; resting spore thick-walled, epibiotic, borne like the sporangium, germination not observed.

A monotypic genus, saprophytic on vegetable debris in fresh water.

Although early stages in the development of this remarkable chytrid were not observed Minden did determine that the young plant consisted of a short somewhat cylindrical or irregular thick-walled main axis that gave rise basally to coarse rhizoids. Beneath the apex of this axis a lateral outgrowth appeared which soon expanded to form a spherical, at first oblique but later nearly upright, body—the rudiment of the sporangium. As this rudiment continued to expand the true apex of the axis was pushed aside and appeared as a blunt or rather angular process on the mature thallus. The whole thallus was one-celled and filled with dark, brownish, granular protoplasm, which was mostly collected in the distal expanded part. The latter was then cut off by a cross wall from the rest of the thallus and its contents were cleaved into zoospores. At maturity the sporangia were so large as to be visible to the naked eye. Minden was in doubt as to whether or not he observed the resting spore (Fig. 22 D).

The genus is an interesting one from a phylogenetic standpoint, since in its thallus development it approximates *BlastocladIELLA*, a member of the Blastocladiales. It seems probable, however, that there will be found in the future an inoperculate *Macrochytrium*-like chytrid which will even more closely connect these two orders than does Minden's fungus.

MACROCHYTRIUM BOTRYDIOIDES Minden

Centralbl. f. Bakteriol., Parasitenk. u. Infektionskrankh., Abt. 2, 8:824.
1902; Kryptogamenfl. Mark Brandenburg, 5:386, fig. 30 a-c. 1911
(1915); Falck, Mykolog. Untersuch. Berichte, 2:249, pl. 8, figs.

76-85. 1916

Sporangia broadly ellipsoidal, with a broad rounded apex, sub-spherical or somewhat long-cylindrical, variable in size, the larger ones 300-350 μ long by 200-250 μ in diameter, and the smaller up to 800 μ long by 650 μ in diameter, wall smooth, fairly thick, the outer layer cuticularized, the inner colorless, cut off from the broad

apex of the rhizoidal axis by a concave cross wall; rhizoidal axis stout, 400–450 μ long by 60–90 μ in diameter, divided basally into a rootlike complex of coarse wide-lumened thick-walled richly branched

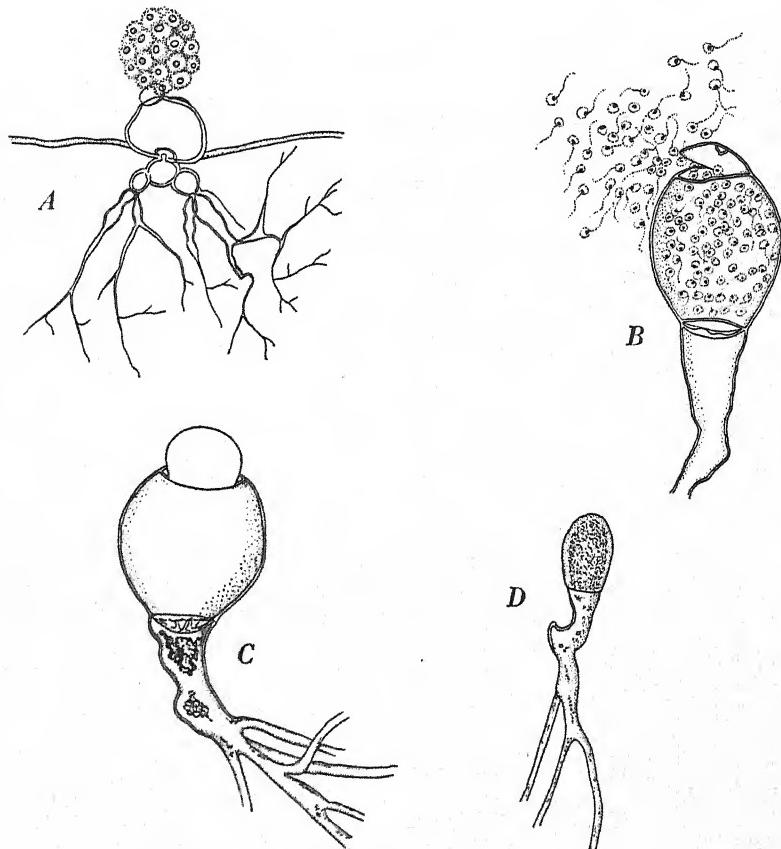


FIG. 22. *Catenochytridium* and *Macrochytrium*

A. Catenochytridium carolinianum Berdan on decaying wheat; epibiotic operculate sporangium, on upper part of which is attached a portion of spore case, is discharging its zoospores; catenulate compound apophysis and rhizoids are within substratum. *B-D. Macrochytrium botrydioides* Minden on submerged fruits: *B*, discharging operculate zoosporangium; *C*, empty sporangium with operculum persistent; *D*, resting spore (?); primary apex appears as kneelike projection on left, terminating rhizoidal axis.

(*A*, Berdan, 1939; *B-D*, Minden, 1916)

rhizoids which are imbedded in the substratum; zoospores up to a thousand in large sporangia, spherical, with a long flagellum, emerging through a broad apical pore formed upon the dehiscence of a broad convex smooth operculum that occasionally bears at the center of its inner wall a short peglike outgrowth, the emerged spores surrounded by a delicate vesicle which ruptures when about one half the size of the sporangium, movement of zoospores at first amoeboid, later, when free of the surrounding bacterial mass, swimming; resting spore (?) borne like the sporangium, contents with globules, germination not observed.

Saprophytic on rotting fruits, especially apples, possibly also on old submerged twigs, Minden (*loc. cit.*), GERMANY; twigs of various trees (*Quercus*, *Abies*, *Fraxinus*, *Alnus*, *Aesculus*), Lund (1934:56, fig. 29), DENMARK; submerged pears, coll. B. Kanouse, communication, UNITED STATES (MICHIGAN).

Lund noted that his fungus, which was 100–558 μ long, was usually collected in pools of stagnant water where there was much decaying vegetable material and where the surface was frequently covered by aquatic angiosperms. It occurred in tufts on the twigs in company with *Blastocladia*, *Rhipidium*, and the like, always covered by bacteria. From these facts he concluded that it did not require much oxygen for its existence. Dr. B. B. Kanouse has frequently found it in the vicinity of Ann Arbor, Michigan, on submerged pears. *Macrochytrium* is the largest of the monocentric chytrids.

SUBFAM. ENDOCHYTRIOIDEAE

Sporangium, rhizoids, and resting spore endobiotic; epibiotic part an evanescent or persistent cyst.

ENDOCHYTRIUM SPARROW

Amer. J. Bot., 20:71. 1933

(Figure 23 A-E, p. 372)

Thallus endobiotic, monocentric, eucarpic, mono- or polyphagous, consisting of the rudiment of the sporangium and the branched rhizoidal system emerging from it, the cyst and penetration tube evanescent or persistent; sporangium operculate, with a discharge tube the tip of which at least is extramatrical; zoospores formed in the sporangium, posteriorly uniflagellate, with a single globule; rest-

ing spore thick-walled, endobiotic, borne like the sporangium, apparently asexually formed, upon germination functioning as a pro-sporangium, the sporangium epibiotic, operculate.

The species are weakly parasitic or saprophytic in fresh-water green algae or saprophytic in decaying plant tissues.

Morphologically, the genus is the operculate counterpart of *Entophyscysis*.

Karling (1937a), who has made an extensive study of *Endochytrium operculatum*, points out that, according to the original description and diagnosis, the genus as first described cannot include a monocentric endobiotic operculate chytrid. This statement, however, fortunately applies only to certain figures, and nowhere in the diagnoses of genus or species is polycentricity implied. The error perpetrated in the figures was due, in fact, as Karling states, to the frequent impossibility of following in the dense algal contents the course of the rhizoids and their relationship to the sporangia.

KEY TO THE SPECIES OF ENDOCHYTRIUM

Sporangia predominantly ovoid or pyriform, smooth

Resting spore filling container; case of the infecting zoospore not persistent

Resting spore entirely smooth-walled *E. ramosum*, p. 369

Resting spore warty *E. operculatum*, p. 370

Resting spore lying loosely in the container, the outer wall scaly;

case of the infecting zoospore persistent *E. pseudodistomum*, p. 371

Sporangia predominantly elongate, obclavate, or triangular and basally lobed, often somewhat apophysate *E. digitatum*, p. 373

ENDOCHYTRIUM RAMOSUM Sparrow

Amer. J. Bot., 20:72, pl. 2, figs. A-G. 1933

(Figure 23 A-E, p. 372)

Sporangium ovoid, subspherical, or sometimes pyriform, up to 35μ in diameter, with a short broad discharge tube which just penetrates the wall of the substratum, wall thin, smooth, colorless; rhizoids extensive, irregularly and profusely branched, ramifying through many cells, often broad (up to 10μ in diameter) at the basal or somewhat lateral place of attachment on the sporangium wall; zoospores spherical or somewhat elongate, $3-5 \mu$ in diameter, pos-

teriorly uniflagellate, with a colorless centric globule, escaping upon the dehiscence of an operculum $7\ \mu$ in diameter and forming for a few moments at the orifice an ellipsoidal motionless mass; resting spore spherical, $20-35\ \mu$ in diameter, with a smooth faintly brownish wall $2.5-3\ \mu$ thick, contents with a large central and several small peripheral globules, germination not observed.

Weakly parasitic or saprophytic in *Cladophora*, UNITED STATES.

Resting spores were found in abundance in old cultures in dead *Cladophora*. These were associated in filaments with the nonsexual stage and were even formed inside evacuated sporangia.

Karling (1937a) has identified the species with one found by him that is saprophytic in various algae and cysts of monads, and considers both to be identical with *Rhizophlyctis operculata* de Wildeman and *Entophysycitis maxima* Dangeard. On the basis of the sporangial stage alone this is justifiable. In Karling's fungus, however, the spherical, ovoid, or slightly ellipsoidal resting spores are $4.5-18\ \mu$ in diameter or $5 \times 7-12 \times 16\ \mu$, and the wall is predominantly rough or warty, only occasionally smooth (Hillegas, 1940). In *E. ramosum*, on the other hand, the resting spores are spherical and larger ($20-35\ \mu$), and the wall is always smooth. Since the character of the wall of the resting spore is ordinarily remarkably constant in a particular species of chytrid and, indeed, in the Phycomycetes as a whole, variation in this respect is unusual and worthy of further study.

To which of these two fungi de Wildeman's *Rhizophlyctis operculata* belonged is problematical, since only the sporangia were found. The same may be said of Dangeard's *Entophysycitis maxima*, which Karling considers synonymous with de Wildeman's and his own fungi.

ENDOCHYTRIUM OPERCULATUM (de Wild.) Karling

Amer. J. Bot., 24:353, figs. 1-53. 1937

Rhizophlyctis operculata de Wildeman, Ann. Soc. Belge Micro. (Mém.), 19:108, pl. 4, figs. 1-9. 1895.

(?) *Entophysycitis maxima* Dangeard, Le Botaniste, 24:242, 1 fig. 1932.

"Zoosporangia hyaline, smooth, almost spherical, $4-140\ \mu$, broadly and narrowly pyriform, $5 \times 7-60 \times 150\ \mu$, ovate, egg- or spindle-shaped, elongated, tubular and cylindrical, occasionally obclavate or irregular and plurilocular with one to several thick exit

papillae or tapering tubes of varying length, 15–75 μ , and diameter, 5–20 μ ; operculum spherical, 4–8 μ , or oval, 4 \times 5–6 \times 7 μ . Zoospores hyaline, spherical or slightly oval, 3–5 μ , with a clear refractive globule in the center. Rhizoidal system usually extensively developed, branched, coarse and irregular, often invading several adjacent host cells and attaining a diameter of from 2–10 μ at its point of insertion on the sporangium. Resting spores hyaline or occasionally with a faint yellow tinge, predominately spherical, 4.5–18 μ , oval or slightly ellipsoidal, 5 \times 7 μ —12 \times 16 μ , smooth, rough, or warty; germination unknown" (Karling, *loc. cit.*).

In various algae, tissues of higher plants, and cysts of *Monadineae*, Karling (*loc. cit.*), UNITED STATES; saprophytic in tissues of higher plants, de Wildeman (*loc. cit.*), FRANCE.

De Wildeman found his fungus only in France (Nancy), not in Belgium.

Successful cultivation on solidified media as well as on a variety of cooked algae and plant tissues has been reported by Karling.

From the figures the operculum is circular and slightly convex, although it is said to be "spherical."

The inclusion of Dangeard's *Entophysycis maxima* in the synonymy is open to question, since no zoospore discharge was observed; the fungus may, in fact, be inoperculate and hence a species of *Entophysycis*.

ENDOCHYTRIUM PSEUDODISTOMUM (Scherffel) Karling

Mycologia, 33:357. 1941

Entophysycis pseudodistoma Scherffel, in Domján, Folia cryptogam., 2:24, pl. 1, figs. 64, 66, 68, 70, 76–81, 85–87, 99, 100, 111. 1936.

Sporangium endobiotic, somewhat ellipsoidal, 17.5–25.4 μ high by 15–25.4 μ broad, with a smooth colorless wall, the extramatrical case of the infecting zoospore persistent, discharge tube 5–15 μ long by 5–7.5 μ in diameter, generally formed on upper part of the sporangium near the place of attachment to the spore case, rarely lateral; rhizoids stout, emerging from the base of the sporangium, strongly developed, much branched, polyphagous, the tips at times becoming extramatrical; zoospores spherical, 5–7.5 μ in diameter, posteriorly uniflagellate, with a colorless centric or eccentric oil drop 1.2–2.5 μ in diameter in the granular vacuolate plasma, escaping upon the

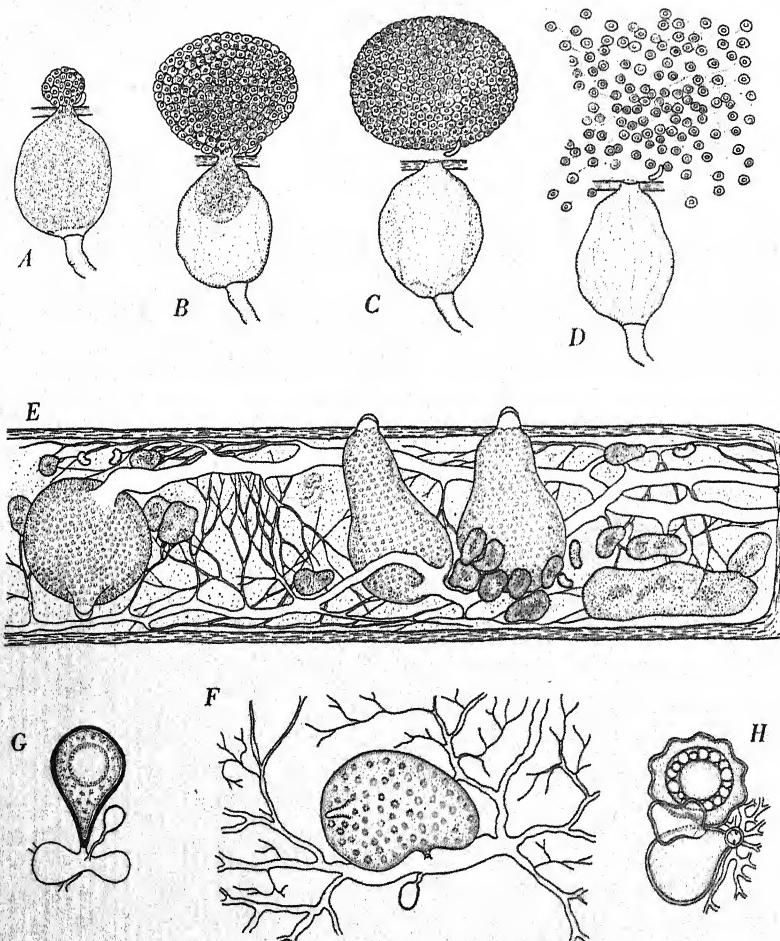


FIG. 23. *Endochytrium* and *Nephrochytrium*

A-E. *Endochytrium ramosum* Sparrow ($\times 380$) in *Cladophora* sp.: A-D, stages in discharge out into the water of zoospores of endobiotic sporangium; E, three plants within alga, bearing mature zoosporangia. F-G. *Nephrochytrium appendiculatum* Karling in *Chara* and *Nitella*: F, portion of thallus bearing mature sporangium; latter is connected by a short isthmus to a long apophysis; persistent thick-walled case of zoospore is attached to apophysis by a short narrow tube; G, resting spore of same species. H. Stellate resting spore of *Nephrochytrium stellatum* Couch ($\times 450$).

(A-E, Sparrow, 1933a; F-G, Karling, 1938a; H, Couch, 1938a)

dehiscence of a circular operculum which terminates the discharge tube and remaining in a motionless group before the orifice, the group slowly moving away and losing coherency and the individuals assuming motion; resting spore endobiotic, nearly spherical, brown, thick-walled, the outer surface provided with irregularly disposed thick slightly reflexed scales, contents bearing a large eccentric oil drop 11 μ in diameter, formed asexually and endogenously in a sporangium-like structure which it partly or completely fills and, like the sporangium, bearing extramatrically the persistent cyst of the infecting zoospore, germination not observed.

Saprophytic in *Spirogyra*, *Zygnema*, HUNGARY.

The presence of an operculum distinguishes this as a species of *Endochytrium* rather than of *Entophysycis*. The binomial should be *Endochytrium pseudodistomum* (Scherffel) Karling, not *Endochytrium pseudodistomum* (Domján) Karling, as given in Karling (*loc. cit.*).

ENDOCHYTRIUM DIGITATUM Karling

Mycologia, 30:307, text figs. 20-37. 1938

"Thalli numerous, intramatrical, monocentric, eucarpic. Zoo-sporangia hyaline and smooth except for one to several blunt digitations at or near the base; formed as an enlargement on the germ tube and delimited from the rhizoidal system by a cross wall at maturity; elongate and obclavate 11 \times 44 μ -18 \times 35 μ , pyriform, 15 \times 22 μ -71 \times 120 μ , obpyriform, irregular, subspherical, somewhat triangular and lobed, with 1-4, usually one, single or branched, straight, curved, undulating, or coiled, tapering exit tubes, 5-18 μ in diameter and 10-275 μ in length, which may occasionally extend 88 μ beyond the surface of the host wall. Operculum spherical or slightly oval, 3.3-5.5 μ . Zoospores hyaline with a clear refractive globule 1.6-2.2 μ in diameter, spherical, 4.4-5.5 μ , posteriorly uniciliate; emerging fully formed and singly, and lying quiescent in a globular mass a short while before becoming actively motile, intermittently amoeboid. Rhizoidal system well developed and richly branched, extending sometimes for a distance of 550 μ , smooth or irregular in contour, 2.7-5 μ in diameter and occasionally digitate at the base. Resting spores smooth, light to medium brown, oval, subspherical, 16 \times 18 μ -10 \times 15 μ , spherical, 20 μ , obpyriform, with a 1.75-2.5 μ thick

wall and a large refractive globule usually surrounded by several small ones; germination unknown" (Karling, *loc. cit.*).

Saprophytic in dead internodes of *Chara coronata*, *Nitella flexilis*, and other algae, UNITED STATES.

IMPERFECTLY KNOWN SPECIES OF ENDOCHYTRIUM

? ENDOCHYTRIUM OOPHILUM Sparrow

Amer. J. Bot., 20:72, text fig. 1 r-s. 1933

Sporangium endobiotic, ovoid, 50 μ long by 30–35 μ wide, with a short papilla which barely penetrates the wall of the egg and which terminates in an operculum about 6 μ in diameter; zoospores spherical or somewhat elongate, 3 μ in diameter, formed in the sporangium, posteriorly uniflagellate, with a single globule, liberated with great rapidity upon the dehiscence of the operculum; resting spore not observed.

Parasitic in rotifer eggs, UNITED STATES.

If further observations confirm the fact that no vegetative system is ever formed the fungus should be removed from *Endochytrium* and placed in a new genus, which would be the operculate counterpart of *Olpidium*.

NEPHROCHYTRIUM KARLING

Amer. J. Bot., 25:211. 1938

(Figure 23 F–H, p. 372)

"Thallus intramatrical, monocentric, eucarpic. Zoosporangia variously shaped, apophysate, with one or more exit papillae or tubes of varying length; formed as an outgrowth from the apophysis and delimited from the latter by a cross wall at maturity. Rhizoidal system coarse, richly branched, and extensive, with occasional elongate, spindle-shaped, intercalary enlargements. Zoospores uniguttulate, posteriorly uniciliate. Resting spores variously shaped, apophysate, thick-walled; formed as an outgrowth from the apophysis; germination unknown" (Karling, *loc. cit.*).

Saprophytic in Characeae and grasses.

Nephrochytrium superficially resembles *Diplophyctis*. It differs from this genus in that "the sporangia and resting spores [of *Diplo-*

phlyctis] are formed as enlargements of the germ tube [whereas] in the present species [*N. appendiculatum*] they develop as protuberances or outgrowths from a transverse, fusiform, spindle-shaped, medianly constricted apophysis. Furthermore, occasional intercalary, spindle-shaped swellings occur in the rhizoidal system, while the zoospore case becomes thickened, amber in color, and persists on the surface of the host cell as an appendage to the sporangia and resting spores" (Fig. 23 F-G, p. 372).

Unfortunately, the critical point as to whether the sporangium is operculate or inoperculate has not been determined in *Nephrochytrium appendiculatum*, the type species. Couch (1938a) has identified with Karling's genus an operculate form with a similar type of development. Because of the frequent parallelisms in body structure known to exist in these fungi, it is impossible to say without a reexamination of Karling's fungus whether Couch's *N. stellatum* and Whiffen's *N. aurantium* should be placed here or in a genus of their own.

KEY TO THE SPECIES OF NEPHROCHYTRIUM

Globule of zoospore colorless

- Apophysis elongate, transverse, spindle-like; resting spore smooth-walled *N. appendiculatum*, p. 375
- Apophysis globose, ovoid, or lobed; resting spore with a stellate wall *N. stellatum*, p. 376
- Globule of zoospore orange *N. aurantium*, p. 377

NEPHROCHYTRIUM APPENDICULATUM Karling

Amer. J. Bot., 25:211, figs. 1-2. 1938

(Figure 23 F-G, p. 372)

"Zoosporangia numerous, hyaline, smooth, sub-spherical, flattened, depressed, usually somewhat kidney-shaped, $8 \times 14 \mu$ — $18 \times 30 \mu$, with 1-3 exit papillae or tubes of varying length. Zoospores hyaline, spherical, 3.5 — 4.5μ , with a large clear refractive globule; cilium approximately 40μ long; zoospore case becoming thick-walled, amber colored, and persisting on the surface of the host cell after germination. Apophysis elongate, transverse, usually spindle-shaped and medianly constricted; rhizoids arising as branches of its ends, extending occasionally over a radius of 600μ and often attain-

ing a diameter of 5–6 μ ; intercalary swellings 4–8 μ in diameter. Resting spores smooth, light to dark amber, usually somewhat kidney-shaped, flattened, depressed, occasionally obpyriform, 10 \times 18 μ —17 \times 26 μ , thick-walled with one or more refractive globules" (Karling, *loc. cit.*).

Saprophytic in cells of *Chara coronata*, *C. delicatula*, *Nitella flexilis*, *N. gracilis*, UNITED STATES.

NEPHROCHYTRIUM STELLATUM Couch

Amer. J. Bot., 25:507, 509, text figs. 1–34. 1938

(Figure 23 H, p. 372)

"Thallus endophytic beneath the cuticle of *Nitella* or sometimes on inner side of cell membrane, monocentric. Each thallus consisting at maturity either of a richly developed rhizoidal system, a more or less spherical apophysis and a zoosporangium, or of a resting body with rhizoids and apophysis. Sporangia roughly disc-shaped from pressure, usually circular in outline in face view but sometimes irregular in outline, particularly when growing with *Coleochaete*, usually with a basal columella which bulges into sporangium; 26–50 \times 29–50 μ ; with a basal, globose, ovoid, or sometimes lobed apophysis, the latter being connected to the sporangium by a narrow isthmus, apophysis 8.4–12.8 \times 14.7–20 μ . The sporangium and apophysis, connected by a narrow isthmus, have an hour-glass-like appearance, the sporangium being much the larger part of the hour glass. Emergence pore formed near columella, usually not tubular but penetrating through the cuticle of the *Nitella*, bursting irregularly but always with a distinct cap. Spores emerging slowly in a spherical mass and remaining quiet for a few seconds at the sporangial mouth; spherical, about 5 μ thick, with a large refractive globule and a very long cilium, 35–40 μ long; zoospore case pyriform, becoming thick-walled, yellowish, and persisting on the surface of the *Nitella*, attached to the apophysis at the isthmus. Rhizoids elaborately developed, much branched, the ultimate branches with blunt tips, attached to the apophysis near the isthmus or more frequently to the isthmus by one main trunk. Resting spores near amber brown, nearly spherical but slightly wider than tall, usually with 8–12 large, rounded protuber-

ances, rarely smooth, wall 2.8-4 μ thick, when ripe with one large oil (?) globule surrounded by a layer of smaller spherical bodies, 10-30 μ wide \times 11-29 μ long, usually 18-21 μ wide \times 16-19 μ long; spore with an empty, basal, usually barrel-shaped, or sometimes irregular apophysis, the walls of which are hyaline or nearly so; barrel-shaped part about 12-19 μ wide \times 8-15 μ long, but much smaller in depauperate specimens, wall about 2.5 μ thick beneath the spore but thinning to a mere membrane at the basal rhizoidal end. The empty zoospore case becoming thick-walled and yellowish and remaining attached to the base of barrel-shaped part. Germination not observed" (Couch, *loc. cit.*).

Saprophytic in cells of *Nitella hyalina*, UNITED STATES.

Distinguishable from *Nephrochytrium appendiculatum* "by the more or less disc-shaped sporangia connected with the nearly spherical apophysis by a narrow isthmus, the columella-like structure at the sporangial base, the irregularly shaped pore through which the spores emerge, and the stellate resting spores"

NEPHROCHYTRIUM AURANTIUM Whiffen

Amer. J. Bot., 28:41, figs. 1-26. 1941

"Thallus monocentric, consisting at maturity of a much branched rhizoidal system, an empty apophysis and an orange-colored zoosporangium. Zoosporangia spherical, cylindrical, or much lobed, 12-54 μ \times 16-62 μ . Exit papillae, one or more in number, closed by a circular cap, which is pushed out by the emerging zoospores. Apophysis, 6-23 μ \times 7-30 μ , typically spherical, developing as an enlargement of the unbranched portion of the germ tube. Rhizoidal system, colorless, extensive, much branched, continuous with the apophysis. Zoospore case orange-brown in color, attached to the apophysis by its germ tube. Zoospores, 4-4.8 μ , spherical, posteriorly uniciliate, each with a single orange-colored oil globule, emerging in a spherical mass and remaining quiescent at the mouth of the exit papilla for several seconds before swimming away. Resting spores unknown" (Whiffen, *loc. cit.*).

Saprophytic on grass leaves, UNITED STATES.

IMPERFECTLY KNOWN GENUS OF THE CHYTRIDIACEAE

? HAPLOCYSTIS SOROKIN

Bull. Soc. Nat. Kazan, 4(3):11. 1874

Thallus epibiotic, monocentric, obpyriform, with a short narrow stalklike base, apparently without a vegetative system, superficially attached to the substratum, the contents divided by successive cleavage into thirty-two parts which rotate within the operculate sporangium and conjugate in pairs; swarmers (planozygotes) biflagellate, emerging upon the dehiscence of a broad operculum, movement hopping; resting stage not observed.

A monotypic marine genus on submerged wood.

? HAPLOCYSTIS MIRABILIS Sorokin

Bull. Soc. Nat. Kazan, 4(3):11, pl. 1, figs. 44-55. 1874

Sporangium 117 μ high, wall thin, smooth, swarmers sixteen, spherical, 11 μ in diameter, with a refractive globule, upon germination enlarging to form a new sporangium.

On wood, ITALY (VENICE).

A fungus with such a remarkable life history is not improbable, but certainly needs validation by further observations.

MEGACHYTRIACEAE^{1,2}

Thallus epi- and endobiotic, or free in the medium, only the tips entering the substratum, polycentric, either rhizoidal, extensive, and much branched, with intercalary swellings, or broadly tubular, hypha-like, not distinctly rhizoidal, with swellings; zoosporangia operculate, formed from terminal or intercalary swellings; zoospores posteriorly uniflagellate; resting spores thick-walled, apparently asexually formed, upon germination producing zoospores.

Saprophytic in vegetable debris, one genus (*Megachytrium*) saprophytic and possibly parasitic on *Anacharis*.

¹ Any family or subfamily names formed by using the older genus *Nowakowskia* as a basis result in combinations which are too polysyllabic to be tenable.

² See the new genus *Cylindrochytridium* Karling, Bull. Torrey Bot. Club, 68: 382. 1941.

This family includes all polycentric operculate chytrids except *Tetrachytrium* and *Zygochytrium*. These two genera are placed at the end of the family (see pp. 387-390). When further observations validate them (particularly *Tetrachytrium*) each should, perhaps, be put in a family of its own, since they possess radically different types of sexual reproduction (see under "Sexual Reproduction," p. 54).

KEY TO THE GENERA OF THE MEGACHYTRIACEAE¹

Thallus forming tenuous strongly tapering rhizoids

Rhizoids septate only where delimiting the reproductive organs

NOWAKOWSKIELLA, p. 379

Rhizoids septate and constricted at intervals as well as where

delimiting the reproductive organs SEPTOCHYTRIUM, p. 382

Thallus forming a broadly tubular vegetative system not tapering

strongly distally MEGACHYTRIUM, p. 384

NOWAKOWSKIELLA SCHROETER

Engler and Prantl, Natürlichen Pflanzenfam., 1(1): 82. 1892 (1893)

(Figure 24, p. 381)

Cladocytrium Nowakowski, pro parte, in Cohn, Beitr. Biol. Pflanzen, 2:92. 1876.

Thallus eucarpic, polycentric, endobiotic, extramatrical, or both, extensive, branched, rhizoidal, bearing irregular swellings, septate turbinate cells, and the rudiments of the zoosporangia and resting spores; zoosporangium operculate, generally apophysate, intra- or extramatrical, internally proliferous; zoospores posteriorly uniflagellate, with a single globule, escaping through a sessile pore or a discharge tube, generally undergoing a period of rest at the orifice before swimming away; resting spore borne like the sporangium, thick-walled, germination not observed.

A genus containing species saprophytic in the decaying parts of higher plants and in the gelatinous sheath of *Chaetophora*.

The vegetative system is ordinarily very extensive and profusely branched and bears numerous irregularities. It may be entirely within the substratum or form in addition an extensive extramatrical growth. The commonest species, *N. elegans*, may generally be collected by baiting aquatic sites, or even water cultures containing vegetable trash, with bits of grass or corn stem.

¹ See also *Tetrachytrium* and *Zygochytrium*, pp. 387-390.

KEY TO THE SPECIES OF NOWAKOWSKIELLA¹

- Resting spores not formed *N. elegans*, p. 380
 Resting spores formed, developed from marginal cells of a pseudo-parenchymatous tissue *N. ramosa*, p. 382

NOWAKOWSKIELLA ELEGANS (Nowak.) Schroeter

Engler and Prantl, Natürlichen Pflanzenfam., 1(1):82. 1892 (1893)
 (Figure 24)

Cladochytrium elegans Nowakowski, pro parte, in Cohn, Beitr. Biol. Pflanzen, 2:95, pl. 6, figs. 14-17. 1876.

Nowakowskella endogena Constantineanu, Revue Gén. Bot., 13:387, fig. 83. 1901.

Sporangium terminal, occasionally intercalary, when free being spherical, ovoid, pyriform, or oblong, when endobiotic often assuming the shape of the confining cell, 16-40 μ or more in width, generally apophysate, with or without a discharge tube, wall thin, smooth, colorless, proliferating, operculum smooth or umbonate; rhizoidal system strongly polycentric, profusely developed, with irregular expansions, 1-10 μ or more in width, tips delicate, septate turbinate cells occasionally formed; zoospores spherical, 5-7.5 μ in diameter, with a large colorless globule and a long flagellum, escaping upon the dehiscence of the operculum, 5-7 μ in diameter, and forming a temporary motionless compact mass at the orifice, imbedded in or surrounded by mucilaginous material, movement swimming or amoeboid; resting spores not observed with certainty.

Saprophytic in the gelatinous sheath of *Chaetophora*, Nowakowski (*loc. cit.*), GERMANY; decaying leaves of *Alisma Plantago-aquatica*, Constantineanu (*loc. cit.*), RUMANIA; boiled grass culms, Matthews (1928:229, pl. 34), cultivated on seeds and corn stem, Sparrow (1933a:70, text fig. 2), grass leaves, Couch (1939a), UNITED STATES; in leaves of *Anacharis* and grass, Sparrow (1936a:453, pl. 17, fig. 17), ENGLAND.

Constantineanu's fungus is said to differ from *Nowakowskella elegans* in being endobiotic and in the sporangium's possessing a discharge tube. Both of these are variable characters and of question-

¹ See also *Nowakowskella profusa* Karling (*Bull. Torrey Bot. Club*, 68:381. 1941) and *N. hemisphaerospora* Shanor (*Amer. J. Bot.*, 29:174. 1942).

able taxonomic worth in distinguishing species. The form called *N. endogena* by Domján (1936:51) appears from the character of its resting spores more nearly related to *N. ramosa*.

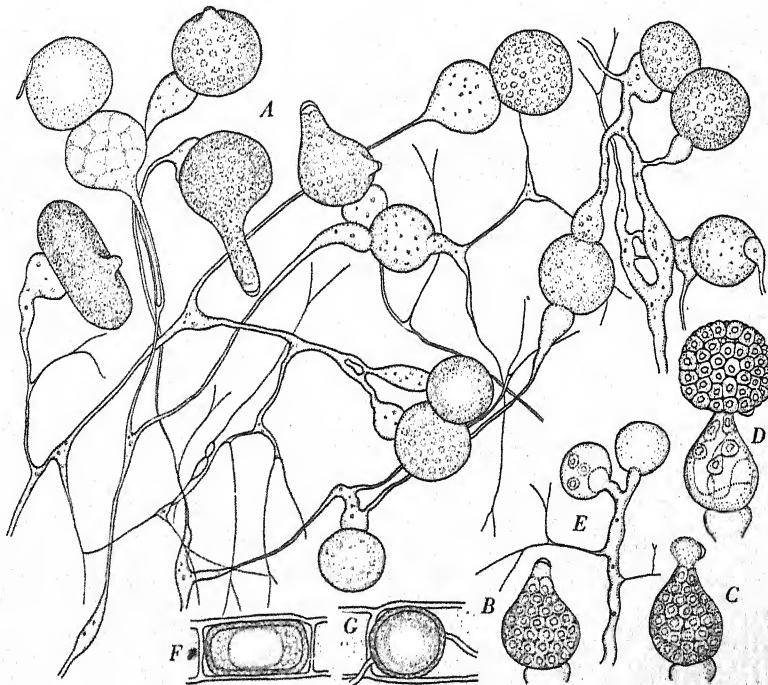


FIG. 24. *Nowakowskella elegans* (Nowak.) Schroeter

A. Portion of extramatrical part of strongly polycentric plant. B-D. Stages in discharge of sporangium. E. Portion of small plant with two sporangia. F-G. Endobiotic resting spores found associated with sporangial plants. (All $\times 600$.)

(Sparrow, 1933a)

Thick-walled spherical or ellipsoidal apophysate colorless resting spores with fatty contents were found associated with the sporangia in the British material. From the fact that they were borne on a polycentric rhizoidal system it is possible that they may belong to the species, but further observations are necessary to determine this point with certainty.

NOWAKOWSKIELLA RAMOSA E. J. Butler

Mem. Dept. Agr. India, Bot. Ser., 1:141, pl. 10, figs. 3-10. 1907

"Mycelium copious, intra- and extra-matrical, of much branched hyphae, irregular in size, from less than 1μ to 45μ (4.5μ ?) in the swollen parts, old hyphae thick walled, anastomosing; sporangia terminal or intercalary, $25-45 \mu$ in diameter, spherical or pyriform, usually with a swollen apophysis, opening by an operculum; zoospores formed before the operculum opens, escaping in a mass or singly, spherical, with one cilium and a large oil drop; durable spores formed in a thin-walled pseudoparenchyma, smooth, with a moderately thick wall, yellowish, $18-25 \mu$ in diameter" (Butler, *loc. cit.*).

Saprophytic on rotting stems of *Triticum vulgare*, Butler (*loc. cit.*), INDIA; tissues of *Typha (angustifolia ?)*, Domján (as *Nowakowskia endogena*; 1936:51, pl. 1, figs. 89, 98, 108-109, 112-124, 126-127, 133-136, 143-150, 156-159, 166, 168-169, 175-179), HUNGARY.

Domján's fungus differs from Butler's only in that the resting spores were occasionally somewhat angular.

Butler describes the development of the resting spores as follows: "Certain hyphae commence to proliferate, either at their ends, or laterally, growing out into large, irregular cells. New cells are formed from these, both by proliferation, and by division of existing cells. In this manner a thin-walled mass of angular cells is formed, sometimes of considerable size. The marginal cells of this swell up into spherical bodies, which thicken their walls to become resting spores. As the process advances, the first formed cells are emptied of their contents, which apparently go to form new cells. As a final result, a group of resting spores is produced, joined together by the thin-walled parenchymatous tissue of the mass." This peculiar process has also been observed by Domján.

SEPTOCHYTRIUM BERDAN

Amer. J. Bot., 26:461. 1939

(Figure 25 C, p. 385)

"Rhizomycelium intramatrical, predominantly polycentric, consisting of elongate, septate and constricted filaments, intercalary swellings and finely branched rhizoids. Zoosporangia variously shaped, operculate, terminal and intercalary, with one (occasionally

several) neck of variable length. Zoospores posteriorly uniciliate, emerging in a globular to ovoid mass and lying quiescent for a few moments before swimming away; method of swimming rapid and darting. Resting spores terminal or intercalary, formed in the same position as the sporangia or from the intercalary swellings; germination through a pore in the wall directly into an operculate zoosporangium similar to the evanescent one or into a tube at whose tip the contents are concentrated and cut off by a cross wall to form the zoosporangium" (Berdan, *loc. cit.*).

Saprophytic on various plant parts.

SEPTOCHYTRIUM VARIABILE Berdan¹

Amer. J. Bot., 26:461, fig. 2. 1939

"Zoosporangia hyaline to pale brown, spherical, 4–150 μ in diameter (often 75–150 μ , average 45–60 μ) with a very short, broad papilla or neck, ovate, egg-shaped, broadly pyriform, 10 \times 15 μ —180 \times 220 μ (commonly 100 \times 150 μ) with neck 4 μ –60 μ wide, obclavate to flask-shaped, 2 \times 6–35 \times 360 μ , bell-shaped, irregular, flattened and depressed with one (rarely several) broad exit papilla or neck of varying diameter and length; zoosporangia delimited by true septa at maturity, sporangial wall smooth when young, striated or layered at maturity, wrinkled when empty; orifice of operculum circular, 1–16 μ in diameter, or slightly oval, 4 \times 6–6 \times 10 μ . Zoospores hyaline, spherical to oval, 4–6 μ , with a single refractive globule, .7–3 μ (usually 2 μ) in diameter; cilium 30–45 μ long. Rhizomycelium coarse, extensive (20 μ —1 cm.), richly branched, with constrictions and septations or trabeculae extending partially or entirely across the rhizoids; inserted on the sporangia at 1–12 points; diameter at point of insertion .4–10 μ . Intercalary swellings usually persistent as empty or partially empty enlargements of the rhizomycelium but often becoming enlarged and transformed into secondary or tertiary zoosporangia or into resting spores, occasionally acting only as a very large, primary centre of organization of the thallus and sometimes seeming to divide into 2 cells one of which enlarges and becomes a zoosporangium or resting spore while the other remains as a sort of apophysis. Treatment with chlor-iodide of zinc giving a pronounced violet colour in the sporangial walls and intercalary

¹ See also Berdan, Amer. J. Bot., 29:260. 1942.

swellings. Resting spore light to dark amber, spherical 4–60 μ diameter, ovoid 4×6 — $50 \times 65 \mu$, or elongated, $10 \times 35 \mu$, thick-walled, smooth, layered, or with outer coat rather irregular, usually with one large refractive globule and numerous smaller ones; zoosporangia formed by direct germination of the resting spore, spherical, pyriform, ovate, etc., usually smaller than the resting spore, those formed indirectly at the end of a tube oval, round, pyriform or clavate; tube wide and saccate or narrow and long with twists and coils, $7\text{--}26 \mu \times 10\text{--}450 \mu$ " (Berdan, *loc. cit.*).

Saprophytic on various grasses, wheat, rye, oats and corn leaves and narcissus root tips, UNITED STATES, CANADA.

MEGACHYTRIUM SPARROW

Occ. Papers Boston Soc. Nat. Hist., 8:9. 1931; Amer. J. Bot., 20:73. 1933
(Figure 25 A-B)

Thallus epi- and endobiotic, strongly polycentric, eucarpic, consisting of much-branched broad tubular occasionally septate hypha-like filaments bearing at frequent intervals the swollen rudiments of the sporangia or resting spores; sporangia operculate, intercalary or borne at the tips of short lateral branches; zoospores posteriorly uniflagellate, with a single globule, formed in the sporangium; resting spore thick-walled, usually intercalary, contents with globules, upon germination functioning as a prosporangium and forming externally an operculate zoosporangium.

A monotypic genus, found thus far only on *Anacharis*.

By reason of its tubular polycentric vegetative system the genus represents an operculate counterpart of the inoperculate *Hypothymium*. The complete development of the thallus is not known. Because of the opaque character of the host difficulty was encountered in tracing it. The zoospore upon germination gives rise to a rather broad undulating "hypha" which, as it grows over the host surface, expands and branches. The "mycelium" ultimately produced varies greatly in diameter, is markedly undulate, and shows in the younger stages of development a tendency to follow the region of juncture of the host cell walls. The latter fact would seem to suggest some type of pectin relationship. Further growth and branching are profuse. The contents of the thallus are finely granular and refractive, with large vacuoles, and are occasionally separated by narrow

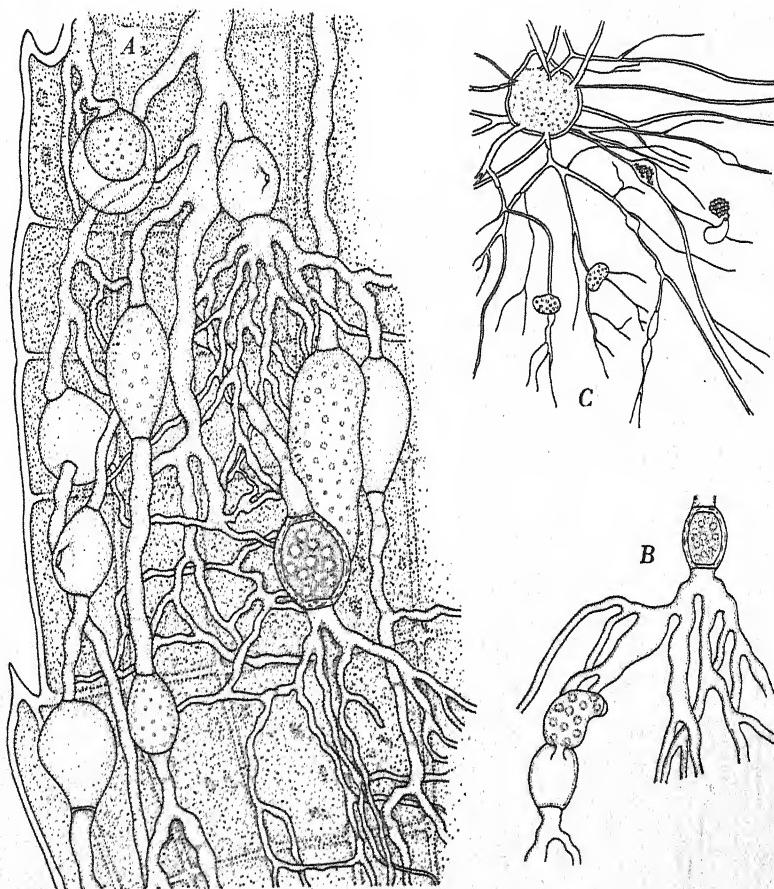


FIG. 25. *Megchytrium* and *Septochytrium*

A-B. Megchytrium Westonii Sparrow on *Anacharis*: *A*, portion of thallus ($\times 600$) bearing zoosporangia, swellings, and resting spores, on *Anacharis* leaf; *B*, portion of thallus ($\times 400$) bearing two resting spores; lower one has germinated and produced an operculate zoosporangium. *C. Septochytrium variabile* Berdan, portion of mature thallus showing large central primary operculate zoosporangium and swellings, and small secondary sporangia.

(*A-B*, after Sparrow, 1933a; *C*, after Berdan, 1939)

cross walls. The ultimate branches are extremely refractive, often fusing laterally with one another in a very characteristic manner. It

is particularly noteworthy that, in contrast to other chytridiaceous forms having a well-developed thallus, such as *Nowakowskella*, the vegetative system never becomes rhizoidal, that is, strongly tapering. In heavily parasitized leaves it is endo- as well as epibiotic, although the method whereby the fungus gains entrance to the host has not been ascertained. On the stouter portions of the threads large broadly fusiform or irregular swellings delimited by cross walls are produced (Fig. 25 A). These may develop either into sporangia or resting spores. The latter may germinate after little or no resting period. In this process the wall is partly assimilated and a sporangium is formed on the outside of the resting spore (Fig. 25 B). Zoospores arise in the usual manner. The ordinary sporangia originate as somewhat pyriform terminal enlargements of the filaments. When mature they are variable in shape and sometimes have a slightly inflated apophysis. Proliferation has been noted in a few instances.

MEGACHYTRIUM WESTONII Sparrow

Occ. Papers Boston Soc. Nat. Hist., 8:9. 1931; Amer. J. Bot., 20:73, pl. 3,
figs. A-E. 1933

Thallus at first entirely epibiotic, later also endobiotic, consisting of a profusely branched extensive tubular undulating hypha-like vegetative system whose main axes are up to $5-7 \mu$ in diameter and whose smaller ones are about 3μ , and of numerous terminal or intercalary swellings; sporangia spherical or clavate but more often irregular, with or without a single short discharge tube, varying greatly in size, usually about $15-50 \mu$ long by $10-30 \mu$ wide, sometimes apophysate, rarely proliferating, wall thin, smooth, colorless; zoospores spherical, 5μ in diameter, with a small colorless centric globule and a long flagellum, escaping upon the dehiscence of a convex operculum $3-5 \mu$ in diameter; resting spore broadly ovoid with truncate ends, with a thick smooth wall, 20μ long by 15μ wide, contents with globules, germ sporangium operculate.

Parasitic on *Anacharis canadensis*, UNITED STATES.

This remarkable fungus caused a pronounced discoloration and disintegration of the leaves of *Anacharis*.

TETRACHYTRIUM SOROKIN

Bot. Zeitung, 32:311. 1874; Bull. Soc. Nat. Kazan, 4 (3):15. 1874
(Figure 26 F-M, p. 388)

Zoospore upon germination developing at one pole a cylindrical axis which forms distally a single short reflexed lateral sterile branch and three terminal ones, each of which bears a single operculate sporangium, developing at the opposite pole a lobed holdfast which anchors the plant to the substratum; the thallus polycentric, eucarpic, hypha-like; zoospores (gametes?) four, with a central vacuole (?), posteriorly uniflagellate, matured outside the sporangium in a delicate evanescent vesicle which envelops the extruded protoplasm after the dehiscence of the operculum, conjugating in pairs to form a new sporangial plant; no resting stage formed.

Primarily saprophytic on submerged decaying wood and grass stems.

TETRACHYTRIUM TRICEPS Sorokin

Bot. Zeitung, 32:311, pl. 6, figs. 23-35. 1874; Bull. Soc. Nat. Kazan, 4 (3):15,
pl. 2, figs. 23-35. 1874

Thallus 39-94 μ long, main axis 19-78 μ long by 5-9 μ in diameter, protoplasm grayish blue; sporangium spherical or subspherical, 15-17 μ in diameter, with a terminal colorless operculum having a prolonged conical umbo; zoospores spherical, 11 μ in diameter, bluish with a colorless centric spot, flagellum from two to three times as long as the diameter of the body, movement lively, never amoeboid.

Saprophytic on wood, grass stems, and the like, cadaver of Coleoptera, EUROPEAN RUSSIA (southern part).

Like *Zygochytrium*, which it closely resembles in its development, thallus, and nonsexual reproduction, the species has never been observed since its discovery by Sorokin and doubts as to its authenticity have been freely expressed by mycologists. The blue coloration of the protoplasm has without question added to this skepticism. Other water fungi occurring on woody substrata occasionally show this bluish color and specimens of *Monoblepharis* have been observed in which it has been very pronounced. This would not, however, explain the coloration presumably found also in the fungus growing on the Coleoptera cadaver.

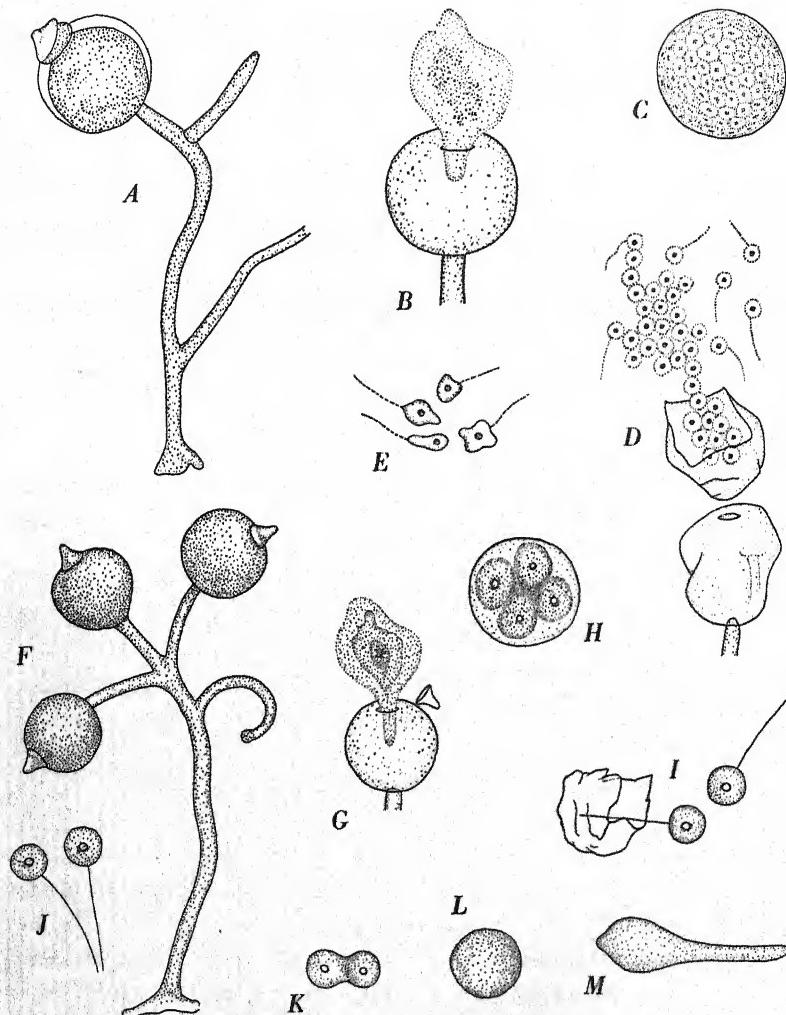


FIG. 26. *Zygochytrium* and *Tetrachytrium*

A-E. *Zygochytrium aurantiacum* Sorokin ($\times 750$) on insect cadavers: A, base and one of the two zoosporangium-bearing branches; B, discharge of uncleaved contents of sporangium; C, contents undergoing cleavage in vesicle at orifice of sporangium; D, liberation of mature zoospores from vesicle; E, mature zoospores. Protoplasm in *Zygochytrium* is golden, with granules of vermillion, and zoospores have a golden plasma with a vermillion globule. F-M. *Tetrachytrium triceps* Sorokin ($\times 750$) saprophytic on bits

Fusion of the zoospores (Fig. 26 J-L) was considered by Sorokin to be a very simple type of fertilization. A somewhat similar occurrence has been reported by Sparrow (1936a:434) in *Chytridium Lagenaria*, where, under poor conditions of nutrition, the receptive thallus, after fusion of the contents of two encysted spores (no merging of the bodies occurred), underwent considerable vegetative development. In this instance, however, unfused spores, in contrast to those of *Tetrahytrium*, were capable of germination.

Further search will probably eventually yield this fungus again, and its true relationships will be established.

ZYGOCHYTRIUM SOROKIN

Bot. Zeitung, 32:308. 1874; Bull. Soc. Nat. Kazan, 4 (3):12. 1874
(Figure 26 A-E)

Zoospore upon germination forming at one pole a cylindrical axis which branches dichotomously, at the opposite pole producing a broad irregularly lobed holdfast which anchors the plant to the outer surface of the substratum, mature thallus polycentric, eucarpic, hypha-like, consisting of the holdfast, main axis, and two dichotomously branched secondary axes, one of the branches of each secondary axis terminating in an operculate sporangium, the other remaining sterile; zoospores posteriorly uniflagellate, with a single globule, formed outside the sporangium in a delicate evanescent vesicle which envelops the extruded protoplasm after the dehiscence of the operculum; resting spore surrounded by an episore and an endospore, formed after the conjugation of the tips of two short lateral opposite branches of the same thallus which became walled off from the branches, germinating by means of a hypha.

On submerged cadavers of insects.

Because of the remarkable combination of chytridiaceous sporangia and zoospores (Fig. 26 A-E) and the zygomycetous type of sexual reproduction (Fig. 2 R-T, p. 46), Sorokin's genus has been

of wood: *F*, complete plant with three sporangia and a recurved appendage; *G*, discharge of uncleaved protoplasm from sporangium; *H*, formation of four zoospores within vesicle at orifice of sporangium; *I*, two of the four zoospores which have escaped at rupture of vesicle; *J-L*, fusion of swarmers in pairs to form zygote; *M*, germination of zygote to form new plant. Color of cytoplasm in *Tetrahytrium* is gray blue.

(After Sorokin, 1874a)

almost universally rejected by monographers and mycologists in general. This rejection has been strengthened by the lack of further observations on the organism. Sorokin's description and figures of the development and reproductive processes are unusually clear and distinct, and there seems no reason for doubting them. Since it is now apparent that the chytrids have evolved a variety of types of sexual reproduction it is not surprising to find a form having a method like that observed in another group of Phycomycetes. Such parallelism is frequent in all types of biological material. No one doubts the relationship of *Polyphagus* to the chytrids, and yet it possesses an unmistakably "zygomycetous" type of sexual reproduction. Such instances, however, do not mean that *Polyphagus* and *Zygochytrium* are related to the Zygomycetes or are even in the same line of fungous evolution.

Repeated collections on the same substrata at the same time of year at the same locality will probably result in the rediscovery of *Zygochytrium*.

ZYGOCHYTRIUM AURANTIACUM Sorokin

Bot. Zeitung, 32:308, pl. 6, figs. 1-22. 1874; Bull. Soc. Nat. Kazan, 4 (3):12, pl. 2, figs. 1-22. 1874

Thalli occurring in orange-red gelatinous masses on the surface of the substratum, each 78-97 μ high, the main axis 58 μ long by 5-7 μ in diameter, protoplasm golden with numerous vermillion granules, wall fairly stout, colorless; zoosporangium ovoid, 19 μ in diameter, bearing an apical somewhat flattened refractive operculum with a prominent conical umbo, wall collapsing after discharge; zoospores spherical, 5 μ in diameter, golden with a centric red globule, escaping from the vesicle by rupturing of the wall, movement lively, shortly becoming amoeboid; resting spore somewhat spherical, 17-19 μ in diameter, exospore blood-red, covered with irregular protuberances, endospore nearly colorless, smooth, contents golden with red granules, resting spore germinating readily (even after twenty-four hours) by the cracking open of the exospore and the elongation of the endospore into a long irregular thick tube (with colorless contents?).

On dead submerged insect cadavers (gnats, flies, wasps), EUROPEAN RUSSIA.

After the formation of sporangia the rest of the plant still contains protoplasm, but there is no evidence that this is eventually used up, even in sexual reproduction.

8894)

BLASTOCLADIALES

THE order Blastocladiales was founded in 1909 by H. E. Petersen to accommodate a single genus, *Blastocladia*, which had been established in 1878 by Reinsch and which up to 1909 had been included in the Saprolegniales. It was apparent to Petersen, even from fragmentary evidence, that the two fungi included in *Blastocladia* differed in several important features from those comprising the Saprolegniales, for they exhibited no cellulose whatsoever in the walls of the thallus and no sexual reproduction, both well-marked characters of the Saprolegniales. Furthermore, Thaxter (1896a) had already shown that the type of zoospore produced by them was quite different in both its internal structure and its method of attachment of the flagella from that found in the older order, although this fact was not stressed by Petersen. In addition, Thaxter's reinvestigation of Reinsch's species confirmed the presence in *B. Pringsheimii* Reinsch of highly peculiar thick-walled punctate resting spores, which were apparently asexually formed. *Blastocladia* had remained a monotypic genus until 1896, when Thaxter, in connection with his observations on Reinsch's species, described a second species, *B. ramosa*. Scarcely two years after the establishment of Petersen's small order Butler (1911) added to it a second genus, *Allomyces*, which differed in several striking features from *Blastocladia*. The distinctiveness of *Allomyces* further justified the segregation of these fungi from the Saprolegniales. In very recent years two other genera, *BlastocladIELLA* (Matthews, 1937) and *Sphaerocladia* (Stüben, 1939), have been added to the Blastocladiales. Detailed monographs on the order have been published by Kanouse (1927) and Indoh (1940). As it stands today the group, though still containing but a small number of genera and species, is composed of clearly related fungi. Furthermore, as a result of a series of recent extraordinarily brilliant discoveries concerning sexuality in these fungi this hitherto small and little-understood group has been raised to a place of high biological importance among the Thallophyta.

Until 1929 no type of sexuality had been convincingly demonstrated in any of the blastocladiaceous fungi. Wherever sexuality had been found among other mycelium-forming zoosporic Phycomyctes it had been clearly oögamous, the diploid phase being

represented by a thick-walled resting oöspore directly formed from the zygote. It is now apparent that as early as 1919 Weston (see Emerson, 1941) had noted in a species of *Allomyces* collected by him in the Philippines that two types of "sporangia" and "zoospores" were produced. Although he suspected that these structures were gametangia and gametes, a decade passed before similar bodies were again observed, this time by Hans Kniep. In 1929 and 1930 Kniep published accounts of the morphology and life cycle of *A. javanicus* in which it was clearly shown that there existed in this fungus a type of sexual reproduction and life history hitherto unknown among any of the fungi. Briefly, Kniep found that his fungus produced posteriorly uniflagellate gametes of two sizes, borne in gametangia of two types on a sexual plant; these free-swimming gametes fused in pairs in the water, and the biflagellate zygote instead of becoming a thick-walled resting structure as in all other known Oomycetes, germinated at once to form a second thallus. This new thallus, though resembling the sexual plant, bore, instead of gametangia, thin-walled zoosporangia and thick-walled punctate resting spores. The zoospores upon discharge from the zoosporangia formed new plants like the parent, whereas the resting spores at germination gave rise to swarmers which reproduced only sexual plants. It was demonstrated, then, that the Blastocladiales, rather than lacking sexuality (in *A. javanicus*, at least), possessed anisogamous planogametic sexual reproduction and alternation of isomorphic (like) generations. The stimulus provided by Kniep's researches has subsequently led to intensive studies of the morphology, sexuality, and life histories of other blastocladiaceous fungi. These have been unusually fruitful and have revealed the existence of isogamous planogametic sexual reproduction (Harder and Sörgel, 1938), and the presence in certain species of *Allomyces* of other types of life cycles (Emerson, 1938a, 1939, 1941). They have also resulted in the recognition of a series of thallus types (Matthews, 1937; Stiben, 1939) which, together with the reproductive structures, unquestionably links this order on the one hand to the Chytridiales and on the other to the Monobpharidales.

So far as is known, all species of the group are saprophytic in fresh water or in soil. Those in water occur most commonly on rosaceous fruits, twigs of ash, birch, oak, and horse chestnut or on bits of animal debris. The precise nature of the substratum of only a

few terricolous species has been ascertained, since these are ordinarily obtained by indirect culture methods. They have been found in nature saprophytic on both plant and animal remains.

Members of the Blastocladiales are characterized morphologically by the possession of posteriorly uniflagellate zoospores, dark-colored resting spores with thick minutely punctate walls, and a more or less well defined basal cell, which is anchored to the substratum by a series of strongly tapering, branching, chytrid-like rhizoids. These rhizoids not only act as holdfasts, but by their extensive growth and profuse branching undoubtedly provide the developing thallus with a well-organized and effective nutrient-gathering system.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

The character of the thallus differs among the different members of the Blastocladiales. As may be seen from the figures and taxonomic descriptions, it varies in character and complexity from that found in a rhizidiaceous monocentric chytrid (Fig. 32 A, p. 414) to that produced by a true mycelium-forming higher fungus. Indeed, the order is remarkable in providing examples of parallelisms of body form with the Chytridiales, Leptomitales, and the higher fungi. Sometimes the thallus may be extremely simple, consisting of either the anchored reproductive rudiment (Fig. 32 A) or the basal cell and rudiment of one or more reproductive structures (Fig. 32 E, Fig. 33 D, p. 434). At other times it is more complex, bearing in addition distal branches of the basal cell (Fig. 33 A) or pseudoseptate branched hyphae of unlimited powers of growth. The walls of the thallus give a reaction for chitin rather than for cellulose (Harder, 1939a, 1939b; Nabel, 1939). The cytoplasm is changeable, differing markedly in the same plant under altered conditions of environment and at various ages. Often it is finely granular and homogeneous or contains dispersed in it minute globules or large clodlike bodies of a fatty nature. At other times it may be either densely packed with irregular refractive granules or reticulately or alveolately vacuolate. It is colorless except in the male gametangia, in the immature resting spores of certain species of *Allomyces*, and in the sporangia of *A. moniliformis*. True cross walls are formed only to delimit reproductive structures. In *Allomyces*, however, peculiar sievelike pseudosepta which resemble true cross walls also occur at intervals along the hyphae.

REPRODUCTION

Nonsexual Reproduction

Nonsexual reproduction is accomplished by posteriorly uniflagellate zoospores which are formed in thin-walled zoosporangia. In *Sphaerocladia* the sporangium is formed from the enlarged reproductive rudiment, derived, as it is in such a chytrid as *Rhizidium*, from the enlarged body of the encysted zoospore (Fig. 32 A, p. 414). In *Blastocladiella* a single sporangium is formed at the apex of the basal cell (Fig. 32 E). In *Blastocladia* (Fig. 33 E, p. 434) the sporangia are sessile, whereas in *Allomyces* they are terminally or laterally placed on hyphal branches arising from the basal cell. In certain species of *Allomyces* secondarily formed sporangia may arise in basipetal succession (Fig. 28 E, G, p. 400).

The zoospores are matured within the sporangium and are liberated through one or more pores formed upon the deliquescence of the papillae. Under certain environmental conditions the first zoospores to emerge are surrounded by a temporary vesicle (Fig. 28 E, p. 400); under other conditions they emerge individually. A peculiar peglike structure which appears to be endogenously formed by the end wall of the sporangium has been found in some species of *Blastocladia*. Its function is unknown. Miss Lloyd (1938) has observed that this plug is divided into an inner and outer part and suggests that it is the inner one which gives rise to the temporary vesicle that often surrounds the zoospores at their emergence. Indoh (1940) has described the papillae formed on the sporangium of *Allomyces* as being projections of the inner sporangium wall. Internal proliferation of the sporangia has been observed in two species of *Blastocladia* (*B. prolifera*, *B. Sparrowii*) (Fig. 33 C, p. 434). The zoospores of all members of the order, with the exception of *Clavochytridium*, are very similar in appearance, internal organization, and type of motility. Although many are spherical when first escaping from the sporangium they assume an ovoid shape during active swarming. The plasma may contain a few anterior minute colorless globules and always bears near the center a dull-gleaming top-shaped or subtriangular structure, the so-called "food body" or "nuclear cap" (Fig. 33 F). In *Sphaerocladia* there is also found a lachrymose structure of the same refractivity as the food body (Fig. 32 D, p. 414), whereas in *Clavochytridium* there is a ring of small oil globules (Fig. 32 I). At the point of emergence of the long slender posterior flagellum a bright refractive

granule, probably the blepharoplast, is often visible. The spore moves in a deliberate and relatively even fashion when swimming. Pronounced amoeboid movement is frequently resorted to under certain conditions, particularly when the zoospores are emerging from the sporangium and when they are nearing the end of their period of swarming. The body of the spore at these times may elongate slightly, become strongly vacuolate, and produce broad irregular anterior and lateral pseudopodia. So far as is known, the zoospores are not capable of repeated emergence. After a varying period of motility they come to rest, round off, and apparently absorb the flagellum into the body. Eventually a slender germ tube appears, which branches distally to form the first elements of the holdfast system. The body of the spore enlarges, the region opposite the point of origin of the rhizoids elongates rapidly, and there is produced either the reproductive rudiment or the basal cell. Further development of the thallus differs with each genus and even with species of the same genus.

The peculiar pitted resting spores so characteristic of the order are unquestionably a device for tiding the plant over unfavorable environmental circumstances. Unlike other parts of the fungus they can withstand drying and freezing and probably high temperatures. Although found for the most part on the zoospore-bearing plant they are also occasionally observed on the gametophyte, if one is formed. Their structure in all instances is identical. In the early stages of their development they resemble in position and shape ordinary zoosporangia. The increasing density and darkening of the protoplasm and the thickening and pigmentation of the wall, however, together with the lack of formation of discharge papillae, soon distinguish them from developing zoosporangia (Fig. 28 F, p. 400). The brownish pigment, characteristic of these resting spores, has in several species of *Allomyces* been found by Emerson and Fox (1940) to belong to the melanin group. At maturity the obpyriform, ovoid, clavate, beaked, or occasionally spherical resting spore is closely enveloped by the thin wall of the container within which it lies. The outer wall of the spore is thick, of varying shades of brown, and regularly perforated by innumerable minute inwardly directed conical pits or pores. The apices of these pores are in contact with a second, thinner, smooth colorless wall which surrounds the cytoplasm. The living contents, although considerably masked by the pigmented

outer wall, are composed of numerous large fat globules imbedded in a finely granular matrix. The resting spores vary somewhat in shape in the different species, but usually have a narrow truncate base and, for the most part, are broadest slightly above the equatorial region (Fig. 28 D, F). The container or hyphal sheath may burst to liberate its resting spore or, more commonly, may persist around the resting spore and be shed with it. Subsequently, upon germination, the container, if persistent, bursts, and the thick outer wall of the resting spore cracks open. Discharge papillae developed on the bulging, exposed, thin inner wall deliquesce to form pores through which posteriorly uniflagellate planonts emerge (Fig. 30 B, p. 407). The type of plant subsequently developed from these swarmers is dependent upon the organism involved.

Sexual Reproduction and Alternation of Generations

Sexual reproduction is known to occur in *Sphaerocladia*, certain species of *Blastocladiella*, and *Allomyces*, but has not thus far been convincingly demonstrated in *Blastocladia* (Lloyd, 1938; Blackwell, 1940; see, however, Bessey, 1939; Blackwell, 1939). In *Sphaerocladia* and *Blastocladiella variabilis*, fusion of isogamous posteriorly uniflagellate planogametes has been observed (see diagram, Fig. 27), whereas in those species of *Allomyces* exhibiting sexuality fusion of anisogamous planogametes appears to be the rule.¹ Isomorphic alternation of generations has been found in all species manifesting sexual reproduction. In *Allomyces* male and female gametangia are formed on the same thallus (Fig. 28 A-B, p. 400), whereas in the other genera, which are monocentric, the gametophyte thallus bears either a + or a - gametangium (Fig. 27). A further discussion of the types of life cycles found in *Allomyces* is presented on page 406.

The elaboration of the life cycle in the Blastocladiales has been thought by some investigators to indicate relationship with the algae. The affinities of the Blastocladiales with the Chytridiales are so much more pronounced, however, that we are forced to conclude that the Blastocladiales and the algae have, in the course of their evolution, merely arrived at similar methods for insuring the beneficial effects of cross fertilization. Although in all those members in which

¹ See, however, McCranie's findings, Figure 29 K-O (p. 404), where isogamy is demonstrated. See also McCranie, *Mycologia*, 34:209. 1942.

sexuality has been discovered similar sporophytes and gametophytes have been produced, yet species may come to light in the future which, like certain brown algae, develop dissimilar ones.

Little is known of the cytology of any of the Blastocladiales with the exception of *Allomyces* (Barrett, 1912a; Lugg, 1929; Hatch, 1935, 1938). Cytological preparations of the zoospores of *Blasto-*

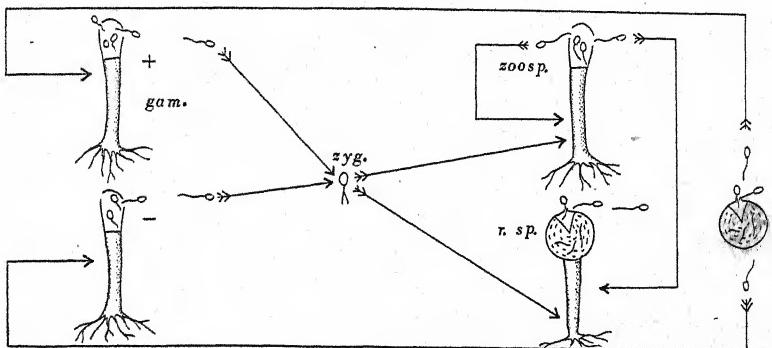


FIG. 27. Diagram of life cycle of *Blastocladia variabilis* Harder and Sörgel

At the left are two gametophyte plants (*gam.*), each bearing a single gametangium from which are emerging isogamous planogametes. Gametes in one gametangium bear an orange pigment, those in the other are colorless. Gametes of opposite signs fuse in pairs to form a biflagellate zygote (*zyg.*), which germinates at once to produce the sporophyte plant. This may be either a zoosporangial plant (*zoosp.*) or one bearing a single thick-walled golden-brown resting spore (*r. sp.*). Zoospores of zoosporangial plant reproduce new sporophyte plants of either type; resting spore upon germination forms planonts which give rise at germination either to + or - gametophyte plants.

Essentially the same life cycle has been described by Stüben (1939) for *Sphaerocladia variabilis* (see p. 416).

(Modified from Harder and Sörgel, 1938)

cladiella simplex are figured by Matthews (1937) and ones of *Blastocladia Pringsheimii* and *Blastocladia globosa* by Cotner (1930a, 1930b). Since *Allomyces* differs so markedly in several respects from other members of the order, its cytology (Fig. 29, p. 404) should probably not be considered representative of the group as a whole.

Information is being accumulated concerning the physiology of members of the order. Species of *Sphaerocladia*, *Allomyces*, and

Blastocladiella have been cultivated on a variety of solid and liquid media in connection with morphological studies, but few analytical data on their nutritional requirements have been published (see Stüben, 1939).

RECENT INVESTIGATIONS ON ALLOMYCES¹

Results of several extensive investigations of the morphology, cytology, life cycle, and distribution of *Allomyces* have been recently published; they have not only revealed facts of great general biological interest but have also increased our knowledge of this genus to a point far beyond that attained for any other member of the order. It seems fitting to interpolate a brief survey of these findings at this point.

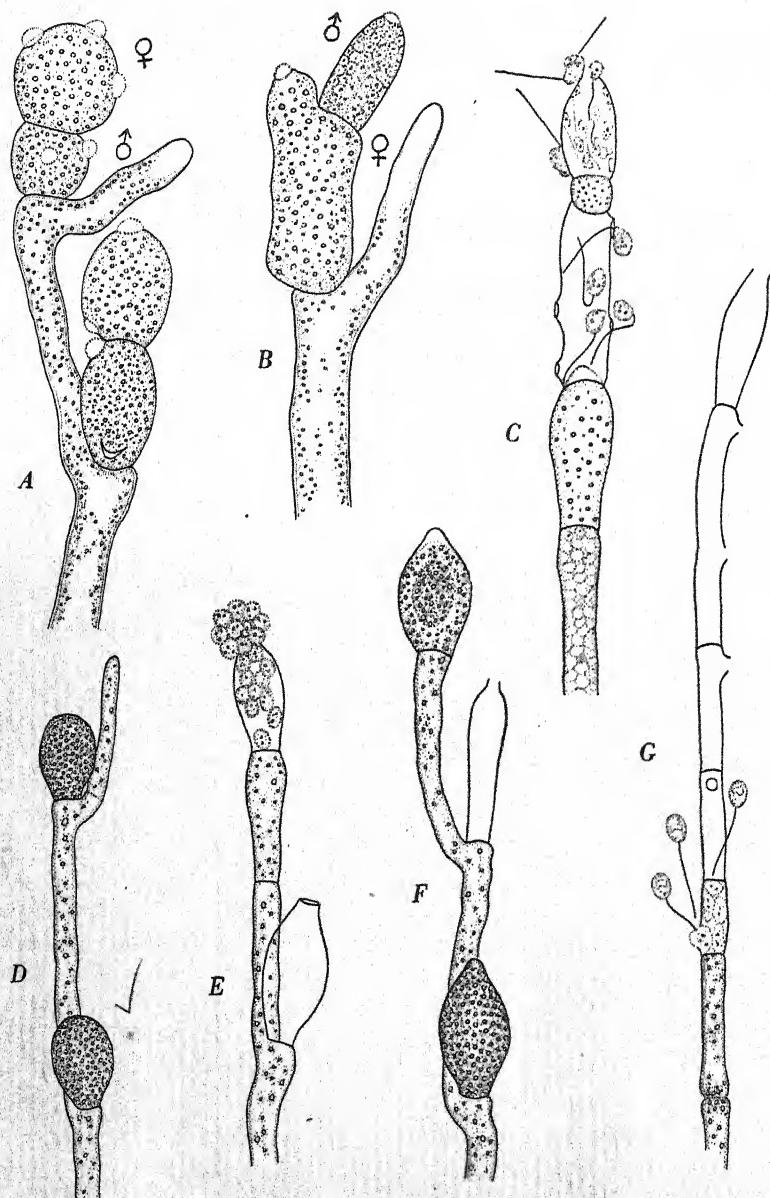
By the use of water cultures prepared with soil samples from various localities throughout the world and "baited" with split hemp-seed, the known distribution of species of *Allomyces* has been increased enormously (see especially Emerson, 1941; F. T. Wolf, 1941). Indeed, it is safe to say that more is known of the geographic distribution of *Allomyces* than of any other aquatic phycomycete. The data on *A. arbusculus*, given by Emerson (*loc. cit.*), is illustrative: In North America it has been found in Illinois, Kentucky, Louisiana, Mississippi, New York, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and Wisconsin; it has also been found in Mexico, Guatemala, Costa Rica, the Dominican Republic, Haiti, Brazil, and Argentina. In Europe it has been collected only in Portugal. In Africa it has been isolated from soil samples from the Belgian Congo, Nyasaland, Uganda, and Cape Province. In the Orient it has been found in soils from India, Ceylon, Burma, China, the Philippine Islands, Bali, and Fiji. The other species of the genus have been less often collected, but they show, as does *A. arbusculus*, the cosmopolitan and predominantly tropical range of the genus.

The sequence of development of the thallus, whether asexual or sexual, is as follows. The swarmer, either zoospore, zygote, or uniflagellate planont from the resting spore, comes to rest at the end of its period of motility, loses its flagellum, and encysts. A germ tube is then produced which branches to lay down the first elements of the rhizoidal system. Soon after, a second, much broader, germ tube grows from the spore body at a point opposite the place of origin

¹ I am greatly indebted to Dr. Ralph Emerson for making available in advance of publication a copy of his important monograph on this genus.

of the rhizoids. This second tube ultimately forms the basal cell, from which arises distally in regular dichotomous fashion a fan-shaped extraordinarily symmetrical complex of hyphae. At occasional intervals along the branches of the young thallus and near the primary diverticulum of the basal cell there are formed discontinuous rings of refractive material which project inwardly from the hyphal wall. These, by centripetal accretion, elongate to produce wheel-like pseudosepta (Coker, 1930). Additional material may be laid down to form a plate punctuated by large radiating triangular openings. Constrictions of the hyphae frequently occur wherever the pseudosepta are located and give a jointed appearance to the thallus. The primary reproductive organs, whether zoosporangia, resting spores, or gametangia, are formed at the tips of hyphal branches, from which they are separated by true cross walls. Secondarily formed zoosporangia and resting spores terminate hyphal branches which, in sympodial fashion, have grown up from beneath the primary organ. Zoosporangia and, rarely, resting spores may also develop in basipetal succession along a hypha.

On the sexual plant the primary gametangia ordinarily appear in pairs, a male and a female, at the tips of the hyphae (Fig. 28 A-C, p. 400), but as growth proceeds, secondary ones, male and female, are alternately formed on sympodial branches or in basipetal succession. The gametangia produce and liberate their gametes in the same manner as do the zoosporangia. During gametogenesis, however, the changes which occur in the aspect of the cytoplasm differ from those found in the zoosporangia. Hatch (1935) states that in *Alloomyces arbusculus* the dense cytoplasm of the contents of the hyphal tip which will give rise to gametangia is gray black, and that this color persists until after the septa delimiting the terminal female and subterminal male gametangia are laid down. The lateral walls of the maturing structures then distend and the color of the male gametangium grows lighter, at first becoming yellowish and later assuming a rusty hue. The female becomes dull gray. With the appearance of the papillae of discharge the contents of the male gametangium turn salmon-pink, whereas those of the female remain unchanged. In both *A. arbusculus* and *A. javanicus* the larger, female, gametes are colorless and resemble zoospores. The male, however, is small, more active than the female, and, so far as is known, always pigmented. It varies with age from faint orange to

FIG. 28. Reproductive structures in *Allomyces*

brick-red, according to the amount of coloring matter accumulated (Emerson, 1941). The pigment has been found by Emerson and Fox (1940) to be composed of gamma-carotene, a relatively rare isomere of carotene. It is located in minute lipoid granules, which in the early stages of development of the gametes are dispersed throughout the cytoplasm of the gametangium. At maturity the colored material becomes more or less localized in the gametes, but never in single globules as in the zoospores of such an aquatic chytrid as *Rhizoclostrum aurantiacum*. Emerson and Fox (*loc. cit.*) point out the relationship of carotene to reproduction in both algae and higher plants and suggest that "such compounds may play important biochemical roles in sexuality and the processes involved in the metabolism of reproduction."

Chance alone seems to decide whether or not male and female gametes, once discharged, will meet and fuse. There is no evidence to indicate that gametes from the same thalli are incapable of doing so. It has been suggested by Hatch (1938) that age plays a part in determining whether fusion will take place. He asserts that whereas it is achieved most readily between recently emerged gametes it becomes increasingly difficult as time elapses. Conjugation most frequently occurs when either one or both of the gametes is temporarily quiescent or exhibiting amoeboid movement. Actual fusion is preceded by a more or less protracted period of intense pseudopodial activity on the part of both gametes. During this period the plasma of the two often becomes strongly vacuolate, and the flagella may wave feebly. Eventually, more or less complete fusion

Explanation of Figure 28

A. Allomyces arbusculus Butler ($\times 330$), tip of hypha of gametangial plant bearing terminal colorless female gametangia and subterminal golden-orange male gametangia. *B. Allomyces javanicus* Kniep ($\times 330$), tip of hypha of gametangial plant bearing a terminal golden-orange male gametangium and a subterminal colorless female one. *C. Allomyces javanicus* var. *japonensis* Indoh ($\times 225$), male and female gametes being discharged and conjugating. *D-E. Allomyces anomalus* Emerson ($\times 225$): *D*, hypha bearing resting spores; *E*, zoosporangia, the terminal one discharging zoospores. *F-G. Allomyces moniliformis* Coker and Braxton ($\times 225$): *F*, tip of hypha bearing discharged zoosporangium, terminal immature resting spore, and, at base, a mature beaked one; *G*, empty basipetal zoosporangia and discharging one.

takes place, after which the zygote swims vigorously about for a time or undergoes a period of amoeboid movement before coming permanently to rest. It then rounds off and encysts; the flagella (according to Hatch, *loc. cit.*) are dehisced; germination then ensues. Cytological investigations by Hatch (*loc. cit.*) of stages in the fusion of the gametes indicate that actual fusion takes place only when the flagella-bearing ends are in opposition. This observation may explain, at least in part, the often prolonged preliminary amoeboid activity. Hatch does not believe that the male plasma is engulfed by that of the female but, rather, that both empty toward a common point of rupture to form the new zygote. He found that nuclear fusion does not occur in most instances until after the flagella of the zygote are cast off and the nuclear caps have dissociated, that is, at the time of germination (Fig. 29 R-V, p. 404). Fused nuclei were seen in zygotes which still bore their flagella. This, Hatch thinks, can be explained by the fact that the orientation of the gamete nuclei in the zygote is such that their still intact nuclear caps do not, as is ordinarily the case, form a barrier to fusion. In most instances the nuclear caps of the two gametes merge soon after conjugation. The initiation of zygote germination is apparently not dependent upon the fusion of the gamete nuclei since in about one half of the specimens examined karyogamy had occurred at this time and in the remainder it had not. It is, however, dependent upon dissociation of the fused nuclear cap, for germination is never initiated until this dissociation is completed. It is asserted, therefore, that the fragmentation of the nuclear cap is the factor causing the zygote to start its development; since Hatch believes the cap to be of chondriosomal origin he therefore concludes: "The fundamental adjustment in germination is thus made by a cytoplasmic structure of chondriosomal origin."

On the asexual plant, the development and cytology of which have been studied by Barrett (1912a), the thin-walled zoosporangia form uninucleate zoospores which are liberated through several pores (Fig. 29 A-F, p. 404). Under some conditions the swarmers emerge individually and swim away at once, whereas under other conditions they escape in a group and remain motionless for a short time, apparently enveloped in a vesicle (Fig. 28 E, p. 400). The resting spore, which is generally formed on the asexual thallus, may at its maturity fall from the plant, still surrounded by its persistent outer hyphal

wall, or this hyphal sheath may burst and the spore drop from it. At germination the contents of the resting structure swell, the outer thick pitted wall cracks, and the inner thin membrane surrounding the living contents bulges out. This thin-walled protruding sporangium then produces several discharge papillae, which deliquesce to form pores through which the planonts emerge (Fig. 30, p. 407). Emerson (1941) states that the whole process of germination may take place within an hour if environmental conditions are favorable.

Certain features in the cytology of various species of *Allomyces* are shown and explained in Figure 29 (p. 404).

It is evident from the investigations of Barrett (1912a), Hatch (1935, 1938), and McCranie that the swarmers, whether zoospores, gametes, or planonts arising from germinated resting spores, are formed in essentially similar fashion. In summarizing the results of a cytological study of gametogenesis in *Allomyces arbusculus* Hatch (1935) states:

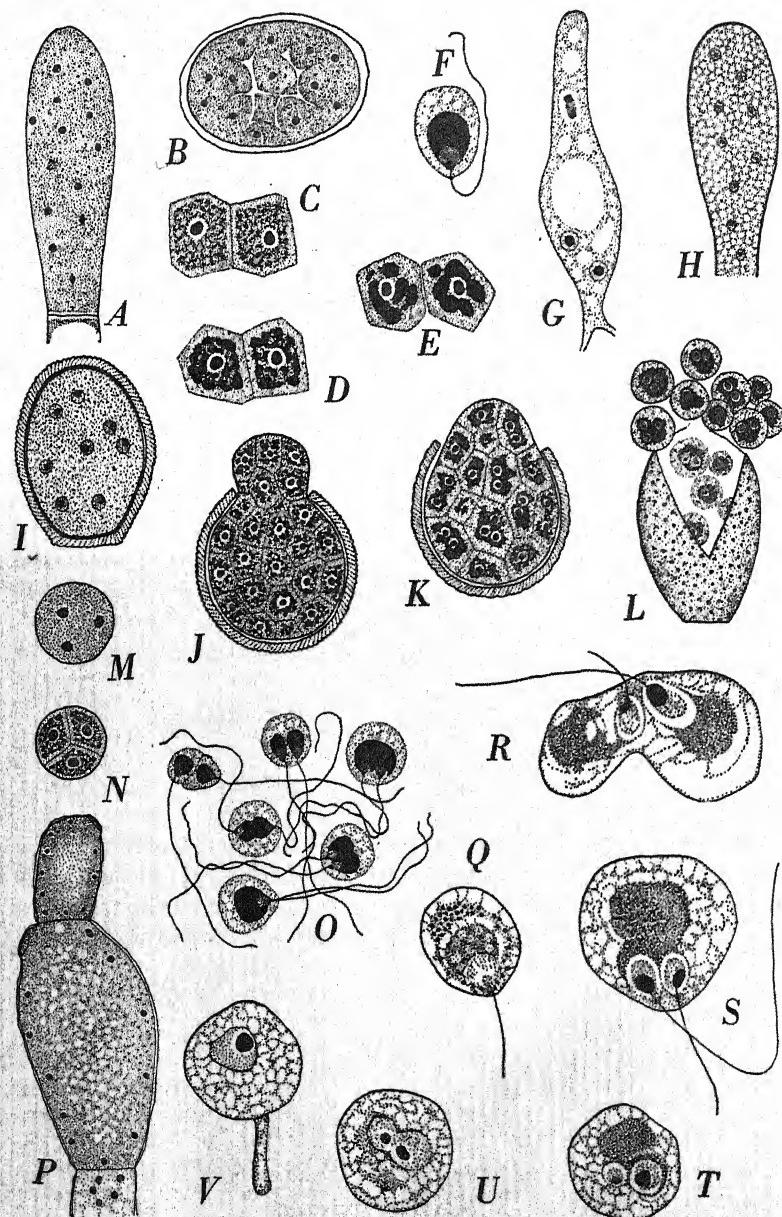
1. In the hyphal tips of *A. arbuscula* there are numerous nuclei, lipoid granules, and chondriosomes. Nuclei and lipoid granules are distributed at random; the chondriosomes are concentrated in the tip. The nuclei have six chromosomes; the lipoid granules are grey-black in colour, small and spherical; the chondriosomes are long and filamentous.

2. When the male and female gametangia are cut off from a hyphal tip the nuclei and lipoid granules are distributed between the male and female gametangium in approximately equal numbers. The chondriosomes segregate unequally, a disproportionately large number going to the terminal, female gametangium.

3. In early gametogenesis the nuclei divide more often in the male gametangium, so that it contains roughly twice as many nuclei as the female. These male nuclei are one-half the size of the female nuclei. The chromosome count, however, is six in the nuclei of both gametangia. These nuclei become the "organization centres" in the formation of gametes, and each collects about itself a sheath of lipoid granules and a tangled mass of fine, filamentous chondriosomes.

4. In late gametogenesis the lipoid granules in the male gametangium change colour, becoming salmon-pink, while those in the female remain grey. The chondriosomes fragment into a cloud of small granules, and these granules subsequently enlarge and fuse to form, first, a reticulate mantle about the nucleus, and finally, a single large mass which becomes appressed to the nucleus in the form of a nuclear cap.

5. The female gamete is two to three times as large as the male; its nucleus

FIG. 29. Cytology of *Allomyces*

Explanation of Figure 29

A-J. Allomyces javanicus Kniep: *A*, immature zoosporangium, some of whose nuclei are dividing; *B*, tangential section of more mature sporangium showing cleavage furrows in center; *C*, two zoospore initials, each bearing a single nucleus; chromatic material which will eventually become aggregated around nucleus to form conspicuous nuclear cap has appeared in cytoplasm; *D-E*, further stages in concentration of nuclear-cap material; *F*, mature zoospore showing large nuclear cap, granular nucleus, and small deep-stained nucleolus, which is connected by a delicate thread to a minute peripheral blepharoplast, to which, in turn, the single posterior flagellum is attached; sequence of formation of nuclear cap and internal organization of swarmer are the same in all the swimming bodies (i.e. zoospores, gametes, etc.) in *Allomyces*; *G*, very young sporophyte plant showing portion of first-formed rhizoids at base and, at tip, germ tube which will produce hyphae; contents are strongly vacuolate and bear two resting nuclei and a dividing one; *H*, hyphal tip forming rudiment of resting spore; note characteristic vacuolization; *I*, very early stage in germination of resting spore; abundant chromatic material characteristically found in cytoplasm of resting spore prior to inception of germination has by now almost disappeared; *J*, germinated resting spore showing enlarged sporangium which has burst resting-spore wall, and nearly mature planonts; latter are in same stage of maturation as are the two zoospores in *D*. *K-O. Allomyces cystogenus* Emerson: *K*, germinating resting spore; note that here, in contrast to *J* (*A. javanicus*), protoplasm has been cleaved into segments bearing from one to several nuclei; *L*, germinated resting spore with cysts bearing from one to several nuclei; *M*, "primary R. S. zoospore," bearing three nuclei; nuclear cap has disappeared; according to McCranie, these zoospores bear no flagella; *N*, segregation of "secondary R. S. zoospores," showing usual aggregation of chromatic material around nucleus; *O*, stages in fusion of swarmers (isogamous gametes) liberated from cysts to form biflagellate zygote, which gives rise to new sporophyte plant. This account of *A. cystogenus* should be compared with interpretation of life history given by Emerson (1941) (see Fig. 31, p. 409). *P. Gametangia* of *Allomyces javanicus* Kniep, showing nuclei in terminal male and subterminal female arranged around periphery. *Q-V. Allomyces arbusculus* Butler: *Q*, female gamete stained with Janus green; with the exception of deep-staining lipoid granules in cytoplasm surrounding nucleus and nuclear cap, structure is like zoospore shown in *F*; *R*, stage in conjugation of male (small) and female gametes; here nuclei are coming to lie side by side without nuclear cap material (dark) between them; *S*, planozygote with two nuclei, as yet unfused, and fused nuclear caps; *T*, resting zygote; flagella have been lost; *U*, zygote in which nuclei are beginning to fuse, the nucleoli still being distinct; nuclear cap has almost completely dissociated; *V*, germinating zygote in which fusion of nucleoli is complete.

(*A-P*, drawings kindly loaned by James McCranie; *Q-V*, Hatch, 1938)

is twice, and its nuclear cap three to four times, as large as that of the male. Its lipoid granules are grey, while those of the male are of a brassy colour.

6. Since the nuclei in the hyphae are genetically the same and are segregated in male and female gametangia in equal number, there appears to be here a peculiar type of differentiation in which the distribution of chondriosomes is of primary importance in the determination of sex.

7. In the visible expression of sexual differences there is a definite quantitative factor in the amount of chondriosomes (nuclear cap) and a qualitative factor in the colour of the lipoid granules.

8. The extranuclear nature of the nuclear cap found in the gametes and zoospores of *A. arbuscula* is demonstrated and its chondriosomal origin described.

A noteworthy series of comparative investigations by Emerson (1938a, 1939, 1941) of a large number of isolates of *Allomyces* from various parts of the world has revealed some extraordinary facts concerning the life cycles of these organisms. It will be recalled that in *A. javanicus*, Kniep (1929) found that the planonts emerging from the resting spores (Emerson terms them "Resting spore zoospores" or "R. S. zoospores") give rise upon germination to sexual plants. The male and female gametes from these fuse in pairs to form zygotes which upon germination produce asexual thalli. An alternation of sexual and asexual phases is, therefore, clearly present (Kniep, 1930). To this "long-cycled" type of life history (Fig. 30) that is characteristic of *A. javanicus* and *A. arbusculus*, Emerson has applied the name "*Euallomyces*."¹ In certain of his isolates, however, he was unable to demonstrate the formation of a sexual phase. A closer study of these specimens revealed the presence of two other types of life cycle. The first, found in *A. moniliformis* Coker & Braxton, in *A. cystogenus* Emerson, and (recently) in *A. neo-moniliformis* Indoh, has been termed the "*Cystogenes*" type (Fig. 31, p. 409). In it the planont (R. S. zoospore) which emerges from the resting spore is large, sluggish, and posteriorly *biflagellate*. It quickly settles down after escape and encysts. In from one to two hours a discharge papilla forms on the cyst and the contents are cleaved into, ordinarily, four small posteriorly uniflagellate planonts. These, after swarming, come to rest, encyst, and at germination form asexual plants. In interpreting this life cycle Emerson suggests that sexual fusion may

¹ "*Euallomyces*," as well as "*Cystogenes*" and "*Brachyallomyces*," shortly to be described, are used as subgeneric names by Emerson (see *Allomyces*, pp. 420-428).

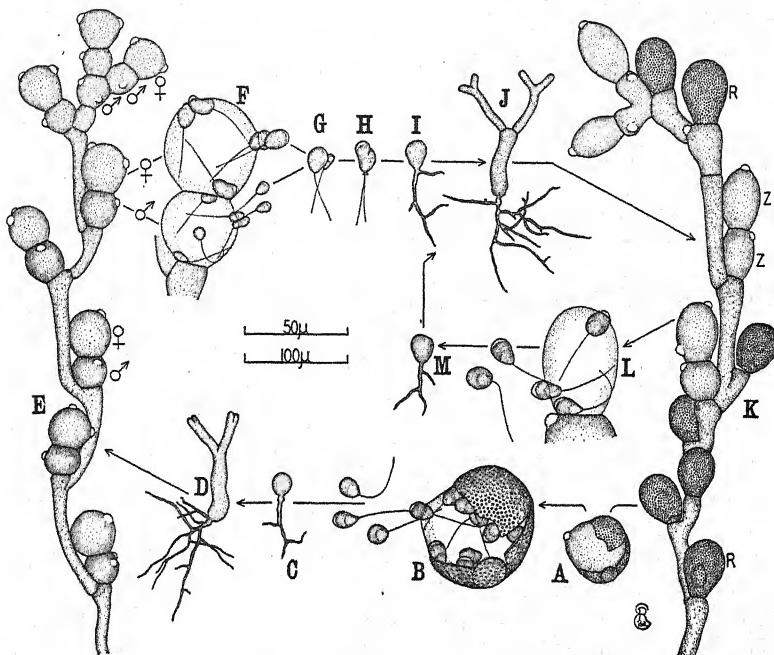


FIG. 30. Life cycle of *Euallomyces* illustrated by *Allomyces arbusculus*
E. J. Butler

"A, germinating resistant sporangium with outer wall split and a papilla of discharge already formed on the inner membrane; B, R. S. zoospores emerging from the germinated resistant sporangium; C, germinating R. S. zoospore; D, young gametophytic plant; E, mature gametophytic hypha bearing female and male gametangia; F, female and male gametes emerging from a pair of gametangia; G, copulating gametes; H, planozygote; I, germinating zygote; J, young sporophytic plant; K, mature sporophytic hypha bearing thin-walled zoosporangia (Z, Z) and heavy-walled resistant sporangia (R, R); L, zoospores emerging from a zoosporangium; M, germinating zoospore" (Emerson, 1941). (Emerson's figures B-C, F-I, L-M, approx. $\times 335$; A, D-E, J-K, approx. $\times 165$; here slightly reduced)

take place during the germination of the resting spore and that the large primary biflagellate planonts are zygotes comparable to those found in *Euallomyces*. This view is strengthened by the frequency with which four planonts are formed by each of the cysts, recalling

the formation of tetrads of spores after meiosis in higher plants. If this interpretation is confirmed by cytological evidence, it will follow that the asexual, zoospore-bearing generation in *Cystogenes* is haploid, rather than diploid as it is in *Euallomyces*. The genus would then possess both haploid and diploid zoospores and resting spores. (See, however, the cytological evidence presented by McCranie in Fig. 29 K-O, p. 404.)

Emerson also found certain isolates which produced neither sexual plants nor cysts. The planonts upon emergence from the resting structures germinated directly into new asexual plants like the parent. In the majority of these isolates further manipulation resulted in the induction of a gametophyte phase similar either to that in *Allomyces javanicus* or to that in *A. arbusculus*. Some isolates even after two years of observation failed to produce sexual plants. Recalling the situation found in *Blastocladia Pringsheimii* by Miss Blackwell (1940), in which precisely the same life cycle was observed, Emerson suggests that there are "brachy-" or short-cycled forms in nature in which the asexual thallus alone is produced. He has termed this life cycle "*Brachyallomyces*" and has placed such isolates in what might be called a "form species" under the binomial *Allomyces anomalus* (Fig. 28 D-E, p. 400).

In addition to the three types of life cycles found as regular and characteristic features of certain isolates, there have been described by Kniep (1929, 1930), Sörgel (1937b), and Emerson (1941) variations or "departures" from the normal life cycle in some isolates of species belonging in *Euallomyces*. The first of these variations is the capacity of the female gamete to develop parthenogenetically. Kniep observed that the female gamete of *Allomyces javanicus* could come to rest, germinate, and form a new sexual thallus, thus simulating a zoospore in function. Both Sörgel and Emerson have confirmed these observations, in Kniep's species as well as in *A. arbusculus*. Sörgel further found that in some instances the female gamete might also give rise directly to asexual plants, a fact verified by Emerson (1941). No instances of germination of the male gamete, however, have ever been noted nor have such gametes ever been seen to fuse with each other.

A second departure noted by Sörgel and Emerson in both the long-cycled species is the formation of asexual plants by planonts from the resting spores. Emerson found that certain of his strains did not

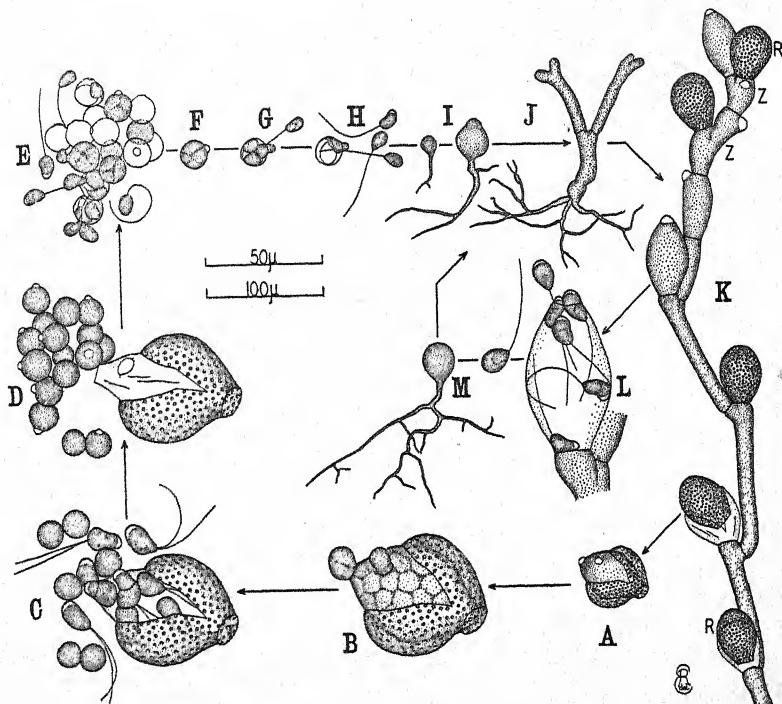


FIG. 31. Life cycle of *Cystogenes* illustrated by *Allomyces cystogenous* Emerson
 "A, germinating resistant sporangium with outer wall split and two papillae of discharge formed on the inner membrane; B, the same (enlarged) just starting to release R. S. zoospores; C, primary R. S. zoospores emerging from the germinated resistant sporangium, some still motile, others already encysted and lacking flagella; D, cysts, clustered at the mouth of the empty resistant sporangium and each with a single papilla; E, secondary R. S. zoospores emerging from cysts; F-H, stages in the emergence of a quartet of secondary R. S. zoospores from a cyst; I, germinating secondary R. S. zoospore; J, young plant; K, hypha of a mature plant bearing thin-walled zoosporangia (Z, Z) and heavy-walled resistant sporangia (R, R); L, zoospores emerging from a zoosporangium; M, germinating zoospore" (Emerson, 1941). (Emerson's figures B-I, L-M, approx. $\times 335$; A, J-K, approx. $\times 165$; here slightly reduced)

regularly produce sexual plants under aquatic conditions and that certain others were induced to do so only after very special treatment. He points out that on this physiological basis we have a series of

forms in both *Allomyces arbusculus* and *A. javanicus* grading from those which regularly produce a sexual stage to those which produce one only after special treatment. The precise reason for this variation from the long-cycled type is not known. Sörgel and Emerson both hint that it may be linked up with environmental conditions, particularly with the amount of nutrient immediately available to the planont on its emergence from the resting spore. No evidence for the fusion of these planonts with each other has ever been observed.

A third departure, by no means uncommon, is the formation of the dark pitted resting spores on the sexual as well as the asexual thallus. Sörgel (1937b) attempts to prove by volumetric studies of the nuclei of plants showing this peculiarity that there are mixtures of gametophyte and sporophyte nuclei within the hyphae. Emerson feels, however, that until there is definite cytological evidence from chromosome counts to confirm the existence of such "mixed hyphae" it is better to assume that both sexual and asexual plants may form resting spores rather than that such structures are restricted to the asexual generation alone. Although Hatch (1935) states that the planonts from these resting spores produce sexual thalli, Emerson feels that this is still a matter of doubt. Further details of these variations from the normal life cycles may be found in the papers of Sörgel and Emerson.

Another aspect of these fungi has been investigated experimentally by Emerson (1941), namely, hybridization and inheritance among species of the *Eualomyces* group. Details of these studies have not as yet appeared. Emerson does give, however, a brief summary of this extremely interesting and, among aquatic Phycomycetes, unique investigation. He says:

Reciprocal crosses were made between *A. arbusculus*, in which the male gametangia are characteristically hypogynous (subterminal in the primary pairs) and *A. javanicus* var. *macrogyrus* in which the male gametangia are always epigynous (terminal in the primary pairs). The arrangement of the gametangia borne on sexual plants derived from the F₁ asexual generation was then studied, and the results, very briefly, are as follows: (1) Gametophyte plants arising from any single F₁ sporophyte (obtained from a single zygote) are of many different sorts, i.e., both parental types, 100% hypogynous and 100% epigynous, segregate out, as well as a series of intermediates ranging from types which show nearly pure epigyny to those showing nearly

pure hypogyny. (2) An exactly similar series of gametophytes can be obtained from any secondary F₁ sporophyte started from a single zoospore discharged from a zoosporangium borne on a primary F₁ sporophyte. These results indicate (a) that the arrangement of gametangia is a quantitative character controlled by polymeric genes, (b) that meiosis does not occur in the zygotes of *Euallomyces*, and (c) that reduction division and segregation of the parental characters takes place after the formation of resistant sporangia on the sporophyte and before the development of mature gametophytes. Hence, although the final interpretation of this work must await the analysis of the F₂ generation, it seems probable that Kniep's original concept is correct and that there is in most, if not all strains of *Euallomyces* a regular alternation between diploid asexual and haploid sexual plants.

These genetical data are of special interest, as Emerson has pointed out, in connection with the problem of the precise location of reduction division in the life cycle of the *Euallomyces* group. Kniep (1930) approached the question by way of volumetric studies of the nuclei of the sexual and the asexual plants. He found that in *Allomyces javanicus* a well-marked ratio of 1:2.12 exists between the average volumes of the nuclei of the sexual and the asexual phases. From this he concluded that meiosis occurs in the resting spores. His work was abundantly confirmed by Sörgel (1936) in *A. arbusculus* ("*A. Kniepii*"). Indeed, even in plants which Sörgel considered to be heteroploid, he found the same constancy in the ratio of nuclear volumes to prevail between the sexual and asexual phases. In connection with this work Sörgel mentions that there are six chromosomes in the gametophyte and twelve in the sporophyte. The only cytological study dealing with reduction division in this genus is that of Hatch (1938), who concludes from his investigations on nuclear behavior in the zygote that meiosis takes place at the first division of the fusion nucleus, at which time the chromosomes are reduced from twelve to six. Although the fusion nucleus is only 6 μ in diameter, the spindle on which the chromosomes are arranged is intranuclear, and the chromosomes themselves are only 1 μ in length, Hatch is able to state with certainty that the first division is reductional. Furthermore, the individual chromosomes can be recognized, and of the haploid six, one is small, one is of medium size, and four are large. The second division, which is sometimes simultaneous in the two daughter nuclei derived from the first division, follows closely the heterotypic division and is equational. The anaphase chromosomes are roughly one half the size of those found

at a similar stage in the first division. Of the four nuclei formed by these two divisions, two are large and two small. The smaller pair, supposedly sister nuclei, degenerate. Confirmation of the cytological observations presented by Hatch will mean, therefore, that plants of both asexual and sexual generations in *A. arbusculus* (and presumably, therefore, in *A. javanicus*) are haploid, and that the diploid condition exists only for a short time in the zygote. Hatch also contends from his study of the zygote that nuclear size (and hence volume) is dependent upon a "nuclear-cytoplasmic ratio" rather than upon the number of chromosomes. If this is confirmed by further work it will invalidate Kniep's and Sörgel's volumetric studies.

It is evident, therefore, that the results thus far published of cytological investigations concerning the place at which reduction division occurs in the *Eualloomyces* life cycle are incompatible with and clearly opposed to the exhaustive volumetric analyses of Kniep and Sörgel and to Emerson's genetical investigations. Although it would seem that greater weight should be attached to results obtained from cytological methods than to those attained by indirect methods, in this instance the small size of the nuclear structures makes their interpretation susceptible to more than the usual amount of error. Indeed, it is no doubt the factor of size which led such experienced investigators as Kniep and Sörgel to attempt an answer by volumetric rather than by cytological methods to the pressing question of the location of meiosis in the life cycle. Considerable confirmatory evidence for the occurrence of reduction division in the zygote rather than in the resting spore will be needed before it can be accepted without reservation.

SYSTEMATIC ACCOUNT

BLASTOCLADIALES

MICROSCOPIC fresh-water and terricolous saprophytic fungi; the thallus coenocytic, eucarpic, sometimes with pseudosepta, true cross walls formed only to delimit the reproductive organs, composed of a system of branched rhizoids that anchor it to the substratum and either a single reproductive rudiment or, more commonly, a basal

cell which bears one or more reproductive structures directly on its surface or on lobes or on extensive nonseptate or pseudoseptate dichotomously, sympodially, or umbellately branched hyphae, sterile setae present or absent, the walls sometimes giving a reaction for chitin, never for cellulose, protoplasm variable in aspect, frequently alveolately or reticulately vacuolate; the fungus sometimes differentiated into similar sporophyte and gametophyte phases, the *asexual* plant bearing one or more inoperculate, uni- or multiporous thin-walled zoosporangia and thick-walled, punctate, generally brownish resting spores borne singly within and completely filling the terminal segments of the hyphae, the *sexual* plant monoecious or dioecious, bearing one or more thin-walled inoperculate uni- or multiporous gametangia; zoospores posteriorly uniflagellate, with a conspicuous subtriangular nuclear cap, monoplanetic, movement swimming or amoeboid, germinating directly to form the asexual plant; resting spores upon germination producing either (a) posteriorly uniflagellate planonts which give rise directly to new asexual plants or to sexual plants, or (b) posteriorly biflagellate planonts¹ which immediately encyst, each of the cysts forming endogenously four uniflagellate planonts that after emerging from the cyst through a pore and swarming germinate to form asexual plants; gametes posteriorly uniflagellate, isogamous or anisogamous, if anisogamous the smaller gamete always containing carotinoid pigment, fusing in pairs to form a biflagellate planozygote which, without a period of rest, germinates to form an asexual plant.

One family is recognized, the Blastocladiaceae, the members of which, so far as is now known, fall into two well-marked groups, one containing the large genus *Blastocladia*, the other, *Sphaerocladia*, *Blastocladia*, *Clavochytridium*, and *Allomyces*. In the first group, *Blastocladia*, the sporangia form a single papilla, with an inwardly projecting peg, and open by a single apical pore. If branches are present they lack pseudosepta and are of slight extent. No sexual reproduction or alternation of generations has yet been found in any member of this genus. In the second group, typically, more than one discharge pore is formed; the branches (lacking in *Sphaerocladia*, *Clavochytridium*, and *Blastocladia*) of the often poorly defined basal cell are pseudoseptate at intervals and are of unlimited growth;

¹ See, however, Figure 29 O, p. 404.

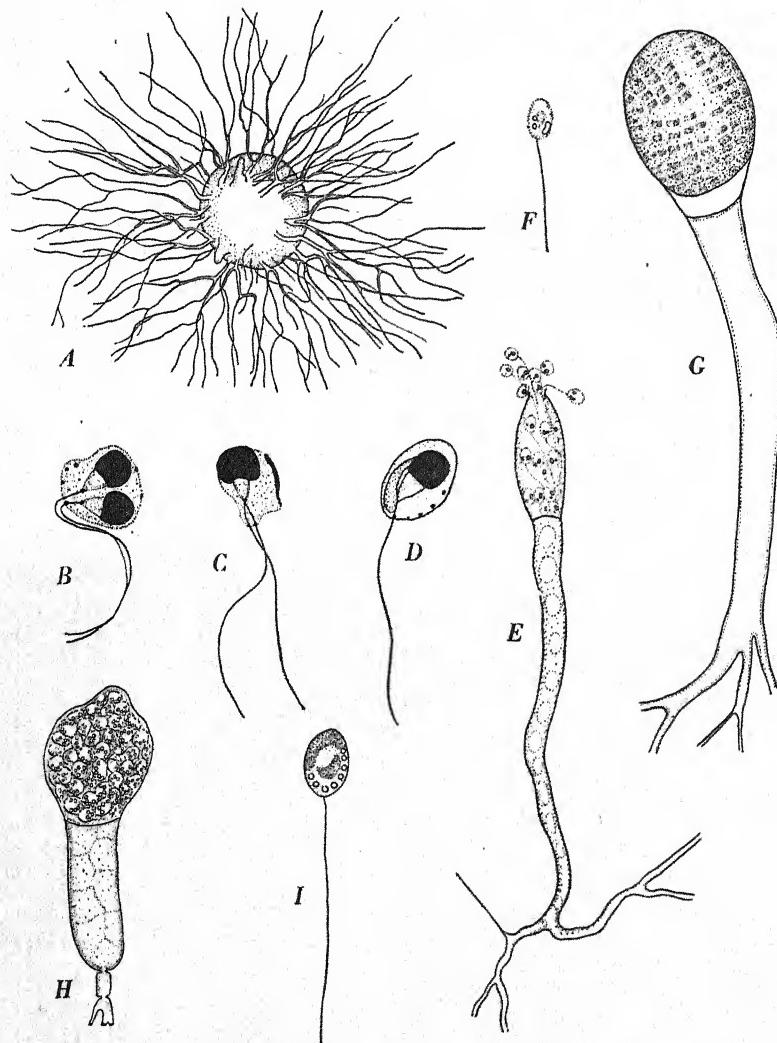


FIG. 32. Blastocladiaceae

A-D. Sphaerocladia variabilis Stüben (*A*, $\times 100$; *B-D*, $\times 1020$): *A*, mature sporangium with two discharge papillae; rhizoids beneath plant are not shown; *B-D*, cytological preparations of swarmers, *B* being two recently fused isogamous gametes, *C*, a zygote, and *D*, a zoospore showing lateral body as well as nuclear cap. *E-G. Blastocladia simplex* Matthews (\times

sexual reproduction, in species where it has been observed, has been accompanied by alternation of isomorphic generations. Further investigations may reveal other points of difference between the two groups or, perhaps, may show that so many intermediate forms exist that their segregation into separate families is not justified.

BLASTOCLADIACEAE

Characters those of the order.

KEY TO THE GENERA OF THE BLASTOCLADIACEAE

- Thallus consisting of a single reproductive rudiment from which the rhizoids emerge, basal cell lacking *SPHAEROCLADIA*, p. 416
- Thallus consisting of a basal cell anchored by rhizoids to the substratum and of one or more reproductive rudiments
- Thallus consisting of an unlobed and unbranched basal cell, bearing distally either a single sporangium or a gametangium or a resting spore
- Contents of the zoospore with a subtriangular nuclear cap *BLASTOCLADIELLA*, p. 417
- Contents of the zoospore with a subtriangular nuclear cap and a lunate ring of refractive globules *CLAVOCYTRIDIUM*, p. 419
- Thallus consisting of a simple or lobed basal cell and rhizoids, with or without distal nonseptate or pseudoseptate secondary axes, bearing an undeterminate number of reproductive organs
- Thallus with an unlobed or unbranched basal cell which gives rise distally and usually dichotomously to cylindrical pseudoseptate branches, setae never formed; zoosporangia with more than one discharge papilla; gametophytes known *ALLOMYCES*, p. 420
- Thallus with a simple lobed or branched basal cell; secondary axes present and lacking pseudosepta or absent, setae present or absent; zoosporangia with a single apical discharge papilla; gametophytes unknown .. *BLASTOCLADIA*, p. 428

225): *E*, small plant with discharging sporangium; *F*, single zoospore (drawn freehand); *G*, plant bearing resting spore. *H-I*. *Clavocytridium stomophilum* Couch and Cox: *H*, basal cell and sporangium ($\times 260$); *I*, zoospore ($\times 660$).

(*A-D*, Stüben, 1939; *H-I*, Cox, 1939)

SPHAEROCLADIA STÜBEN¹

"Planta," Archiv wiss. Bot., 30 (3):364. 1939
 (Figure 32 A-D, p. 414)

Thallus one-celled, consisting of a simple spherical swelling from the surface of which numerous delicate much-branched rhizoids arise, the expanded part converted as a whole into a single reproductive rudiment; sporophyte plant forming from the rudiment either a thin-walled zoosporangium with from one to several short discharge tubes through which the posteriorly uniflagellate zoospores escape, or a thick dark-walled resting spore which upon germination produces posteriorly uniflagellate planohaplonts that give rise to gametophytes; gametophytes similar to the zoosporangial plant but smaller, dioecious, forming either + or - isogamous gametes that fuse in pairs to form biflagellate zygotes, which germinate at once to produce either a zoosporangium-bearing or a resting-spore-bearing sporophyte.

A monotypic genus saprophytic in tropical soil.

Under abnormal conditions the thallus becomes hypha-like and somewhat branched; up to six zoosporangia may form on it. Rhizoids may arise from any part of the thallus, even the reproductive organs.

SPHAEROCLADIA VARIABILIS Stüben

"Planta," Archiv wiss. Bot., 30 (3):364, figs. 1-12. 1939

Sporangium with a thin smooth wall, spherical or more or less ovoid or ellipsoidal, averaging 60μ in diameter on flies, 140μ on peptone agar; rhizoids profusely developed; zoospores emerging through one or several papillae, ellipsoidal, $3.5 \times 4.8 \mu$, the contents bearing in addition to a "food body" a lateral tear-shaped structure; resting spore either ovoid and $13 \times 17 \mu$, the brownish wall 0.5μ thick, or spherical, 110μ in diameter, the wall 2.5μ thick, planohaplonts one half the size of the zoospores, emerging through a prominent papilla which protrudes through a crack in the resting-spore wall; gametophytes similar to the zoosporangial plants but smaller, averaging 106μ on peptone agar, + or - gametes similar to the zoospores but smaller, the zygote biflagellate and germinating at once to form a sporophyte.

In soil, coll. Ulmcke, Mexico.

¹ Couch and Whiffen (*Amer. J. Bot.*, 29:582. 1942) consider *Sphaerocladia* synonymous with *Blastocladiella*.

BLASTOCLADISELLA MATTHEWS¹

J. Elisha Mitchell Sci. Soc., 53:194. 1937

(Figure 32 E-G, p. 414)

Rhopalomyces Harder and Sörgel, Nachrichten Gesell. Wiss. Göttingen, Math.-Physik. Kl., Fachgruppe VI (Biol.), (N. F.), 3(5):123. 1938.
Non Corda et alii.

Thallus consisting of a more or less elongate unbranched basal cell without pseudosepta, forming distally a single reproductive organ, the whole anchored to the substratum by a system of branched holdfasts, walls not giving a cellulose reaction; sporophyte plant bearing terminally either a thin-walled zoosporangium which discharges its fully formed posteriorly uniflagellate zoospores through one or more pores produced upon the deliquescence of papillae, or, in a thin-walled case which it completely fills, a thick-walled punctate resting spore producing upon germination uniflagellate planohaplonts that give rise to gametophytes or uniflagellate planonts which form sporophytes; gametophyte plant similar to the sporophyte, dioecious (heterothallic), forming either + or - isogamous gametes which fuse to produce a biflagellate planozygote that upon germination forms either a sporangium-bearing or resting-spore-bearing sporophyte.

Thus far collected only as a saprophyte in soils in southerly latitudes.

KEY TO THE SPECIES OF BLASTOCLADISELLA

Plant apparently lacking a gametophyte phase *B. simplex*, p. 417

Plant with a definite alternation of generations, gametes isogamous
B. variabilis, p. 418

BLASTOCLADISELLA SIMPLEX Matthews

J. Elisha Mitchell Sci. Soc., 53:194, 1 text fig., pls. 20-21. 1937

(Figure 32 E-G, p. 414)

Basal cell cylindrical, holdfasts delicate, branched, wall thin, smooth; whole thallus, including rudiment of reproductive structure,

¹ See the paper by Couch and Whiffen (as cited p. 416 n.), where three new species, *Blastocladia laevisperma*, *B. aspermoperma*, and *B. cystogena*, are described. The last of these has a life cycle like that described by McCranie for *Allomyces cystogenus*.

30–1005 μ long by 8–40 μ in diameter; sporangium cylindrical to globose, 15–105 μ in diameter, wall thin, smooth, with from one to three discharge papillae; zoospores ovoid to ellipsoidal, 5.5–7 μ long by 3–4 μ wide, with a long posterior flagellum and an anterior ring of refractive globules, emerging in a quickly evanescent vesicle; resting spore borne like the sporangium, 15–180 μ in diameter, surrounded by the thin wall of the container, clavate, with a rounded apex and a truncate base, wall dark brown, thick, coarsely and irregularly reticulate, upon germination forming posteriorly uniflagellate planonts which give rise to zoospore- or resting-spore-bearing thalli, sexuality not known.

On fly cadaver, Matthews (*loc. cit.*) (VIRGINIA), hempseed bait, bog soil (coll. G. R. LaRue), Sparrow (TEXAS), UNITED STATES.

BLASTOCLADIELLA VARIABILIS Harder and Sörgel

Strasburger, Lehrbuch der Botanik für Hochschule, p. 333. 20th ed.
Jena, 1939¹

Rhopalomyces variabilis Harder and Sörgel, Nachrichten Gesell. Wiss. Göttingen, Math.-Physik. Kl., Fachgruppe VI (Biol.) (N. F.), 3 (5): 123, figs. 1–3, fig. 4 B–E. 1938.

Basal cell cylindrical, holdfasts delicate, much branched, wall thin, smooth; sporangium clavate, colorless, wall chitinous, thin, smooth, with several discharge papillae; zoospores ovoid, with a refractive saddle-shaped "food body" and a long posterior flagellum; resting spore borne like the sporangium, spherical, with a thick dark-brown several-layered wall (sculptured?), cracking upon germination and allowing papillae to protrude, which upon dissolution form pores for the escape of numerous posteriorly uniflagellated planonts; planonts upon germination forming thalli like the zoosporangial plants, on each of which is produced either a colorless or an orange-colored clavate gametangium (+ or -); gametes isogamous, + or -, fusing in pairs to form a zygote, which at once produces a sporophyte plant.

Saprophytic in soil, coll. Ulmcke, DOMINICAN REPUBLIC.

From analogy with long-cycled species of *Allomyces*, the pigmented gametangium could be regarded, on this basis alone, as the male, the colorless one, as the female.

¹ Cited by Stüben (1939) as place in which combination is made. Only the genus *Blastocladiella* is mentioned, however, by Harder.

CLAVOCYHYTRIDIUM COUCH AND COX¹

J. Elisha Mitchell Sci. Soc., 55:389. 1939

(Figure 32 H-I, p. 414)

"Thallus monocentric, eucarpic, with an intramatrical rhizomyceum and an extramatrical zoosporangium. Zoosporangia sessile or stalked, with one or more exit papillae. Zoospores posteriorly uniciliate, with two to several small refractive bodies, emerging fully formed and swimming after a few seconds. Rhizoidal system well developed, sometimes septate or constricted, delimited from the zoosporangium by a cross wall at maturity. Walls not turning blue with chlor-iodide of zinc" (Couch and Cox, *loc. cit.*).

In decaying vegetable debris.

The precise relationships of *Clavocyhytridium* to *Sphaerocladia* and *Blastocladiaella* must await the finding of the resting stage and the results of a study of the complete life history. Cox considers *Clavocyhytridium* to be a chytrid. Indoh (1940), however, believes that the genus is synonymous with *Blastocladiaella*.

CLAVOCYHYTRIDIUM STOMOPHILUM COUCH AND COX

J. Elisha Mitchell Sci. Soc., 55:390, fig. 1, pls. 45-46. 1939

"Thallus monocentric; each thallus at maturity consisting of a coarse intramatrical rhizomyceum and an extramatrical zoosporangium. Rhizoids more or less profusely branched, sometimes constricted or ovoid, ellipsoid or cylindrical, sessile or stalked, the length of the stalk variable (up to 320 μ). Spores escaping singly from one or more exit papillae, remaining motionless or becoming amoeboid for a few seconds at the mouth of the sporangium and then swimming away. Spores posteriorly uniciliate (length of cilium 35 to 50 μ), $3.5 \times 6.5 \mu$, ovoid or elliptical, with two to twelve small eccentric refractive bodies. Empty sporangium hyaline, persisting on the surface of the dead host. Resting spores unknown" (Couch and Cox, *loc. cit.*).

Saprophytic on boiled corn and grass leaves used as bait, UNITED STATES.

¹ *Clavocyhytridium* is considered synonymous with *Blastocladiaella* by Couch and Whiffen (see *loc. cit.* on p. 416 n.).

ALLOMYCES E. J. BUTLER¹

Ann. Bot. London, 25:1027. 1911

(Figures 28-31, pp. 400, 404, 407, 409)

Septocladia Coker and Grant, J. Elisha Mitchell Sci. Soc., 37:180. 1922.

Thallus consisting of a cylindrical more or less differentiated trunklike basal cell which gives rise distally to cylindrical dichotomously, subdichotomously, or sympodially branched, blunt-tipped successively more slender pseudoseptate hyphae of indefinite extent on which are borne the reproductive organs, contents often alveolately or reticulately vacuolate, anchored to the substratum by a system of endobiotic branched strongly tapering rhizoids; asexual plant bearing terminally, sympodially, or in basipetal succession thin-walled zoosporangia which discharge their fully formed posteriorly uniflagellate zoospores through one or more pores produced upon the deliquescence of prominent papillae, and persistent or deciduous resting spores with a thick brown punctate outer wall and a thin inner one, the resting spores upon germination producing either (a) posteriorly uniflagellate planonts which give rise directly to new asexual plants or to sexual plants, or (b) posteriorly biflagellate planonts² which immediately encyst, each of the cysts forming endogenously four uniflagellate planonts which, after emerging from the cyst through a pore and swarming, germinate to form asexual plants; sexual plant similar to the sporophyte, monoecious, bearing male and female gametangia terminally in pairs or alternating in basipetal succession, gametes anisogamous, posteriorly uniflagellate, the small male always pigmented, the larger female colorless, the planozygote posteriorly biflagellate and germinating to form the asexual plant.

¹ A great number of isolates of the various species of this genus have been collected. It is impossible in this text to include them all in the sections devoted to geographic distributions. Consequently, only the source of the original isolate or isolates on which the two phases of the particular species are founded or of those pertinent to its interpretation (ones giving rise to synonyms) is noted. Complete data on all isolates are available in Emerson (1941) and F. T. Wolf (1941).

² See, however, the explanation of Figure 29 K-O, p. 404.

In water and soil on plant and animal remains.

Emerson (1938a, 1941) has established three subgenera based on the type of life cycle exhibited. According to his classification, which has been adopted here, these subgenera are:

1. *Euallomyces*, in which the life cycle involves the alternation of like (isomorphic) asexual and sexual generations (Fig. 30, p. 407). The resting spore is persistent on the plant, and the pits in its wall are closely spaced.

2. *Cystogenes*, in which the life cycle apparently consists solely of an asexual phase (Fig. 31, p. 409). The resting spore is deciduous, and its pits are widely spaced. At germination it forms biflagellate planonts which at once produce cysts. From these emerge posteriorly uniflagellate planonts each of which gives rise to a new asexual plant.¹

3. *Brachyallomyces*, in which the life cycle consists of an asexual phase only. The resting spore is like that formed in *Euallomyces*, but upon germination the uniflagellate planonts produce directly new asexual plants (see pp. 406-410 for a fuller discussion of these life cycles).

KEY TO THE SPECIES OF ALLOMYCES

Life cycle of the *Euallomyces* type; pits on resting spore closely spaced

Gametangia when first formed developing in pairs, with the female terminal *A. arbusculus*, p. 422

Gametangia when first formed developing in pairs, with the male terminal *A. javanicus*, p. 423

Life cycle of the *Cystogenes* type; pits on resting spore widely placed

Resting spores mostly beaked or fusiform, cytoplasm often pigmented *A. moniliformis*, p. 426

Resting spores with broadly rounded apex, cytoplasm colorless *A. neo-moniliformis*, p. 427
A. cystogenus, p. 427

Life cycle of the *Brachyallomyces* type *A. anomalous*, p. 428

¹ See, however, the explanation of Figure 29 K-O, p. 404.

SUBGEN. EUALLOMYCES

ALLOMYCES ARBUSCULUS E. J. Butler

Ann. Bot. London, 25:1027, figs. 1-18. 1911. Emend. Hatch, J. Elisha

Mitchell Sci. Soc., 49 (1):163. 1933

(Figure 28 A, p. 400; Figure 30, p. 407)

(?) *Blastocladia strangulata* Barrett, Bot. Gaz., 54:367, pls. 18-20. 1912.

(?) *Allomyces strangulata* (Barrett) Minden, in Falck, Mykolog. Untersuch. Berichte, 2 (2):214. 1916.

(?) *Septocladia dichotoma* Coker and Grant, J. Elisha Mitchell Sci. Soc., 37:180, pl. 32. 1922. ^

(?) *Allomyces arbuscula* forma *dichotoma* (Coker and Grant) Kanouse, Amer. J. Bot., 14:303. 1927.

Allomyces Kniepii Sörgel, Nachrichten Gesell. Wiss. Göttingen, Math.-Physik. Kl., Fachgruppe VI (Biol.) (N. F.), 2 (10):155. 1936; Zeitschr. Bot., 31:402, figs. 2-10. 1937.

Basal cell conspicuous, 100-200 μ long by 60-100 μ in diameter, hyphae copiously sympodially or dichotomously branched, the pseudocells up to 250 μ long by 15-25 μ in diameter; sporangia single or catenulate, broadly ellipsoidal or ovoid, with rounded or truncate ends, 40-70 μ long by 30-40 μ in diameter, forming from one to four discharge papillae; zoospores ovoid, oblong, or ellipsoidal, 12 μ long by 6 μ in diameter; resting spores abundant, ovoid, with rounded apex and truncate base, 28-67 μ long by 16-45 μ in diameter,¹ exospore thick-walled, tawny to reddish brown, minutely punctate, upon germination forming posteriorly uniflagellate planonts; sexual thallus similar to the asexual, gametangia at first terminal in pairs, later catenulate, alternating, the large globose, clavate, or ovoid colorless female gametangium terminal, 40-60 μ long by 16.5-30 μ in diameter, subtended by a short to long cylindrical or barrel-shaped male gametangium 6.6-56 μ long by 13-24 μ in diameter, with faintly golden or salmon-pink contents, female gamete colorless, ovoid, 10-12 μ long by 3.6-7 μ wide, male gamete ovoid or nearly spherical, 6-8 μ long by 4-8 μ in diameter, planozygote biflagellate, upon germination forming the sporophyte.

On insect cadavers (sporophyte only), Butler (*loc. cit.*), INDIA; Barrett (*loc. cit.*), North Carolina No. 2 isolate, gametophyte (coll. A. B. Couch), Coker and Grant (*loc. cit.*), North Carolina No. 1 iso-

¹ From Emerson's data (1941) on this strain, "North Carolina No. 2."

late (coll. W. C. Coker), Emerson (1941), UNITED STATES; Kniep (1930), BALI; CENTRAL AMERICA: MEXICO, GUATEMALA; WEST INDIES: DOMINICAN REPUBLIC, HAITI; SOUTH AMERICA: BRAZIL, ARGENTINA; EUROPE: PORTUGAL; AFRICA: BELGIAN CONGO, NYASALAND, UGANDA, CAPE PROVINCE; INDIA (further isolations by Emerson): CEYLON, BURMA; CHINA; PHILIPPINE ISLANDS; FIJI ISLANDS.

As has been previously indicated, the specific distinctions in this genus depend in great measure on the type of life cycle and, in *Euallomyces*, on the arrangement of the gametangia. Since only the asexual plant was described by Butler and since there are now no living cultures of his fungus, it is impossible to say just what he had. Coker and Matthews (1937) have associated with this species a gametophyte stage described by Hatch (1933) (North Carolina No. 2 isolate) in which the female gametangium is, as in Kniep's isolate from Bali, terminal. It is entirely possible that Kniep's *Allomyces javanicus* was similar to Butler's fungus. Indeed, of four isolates obtained by Emerson (1941) from the same locality in which Butler's fungus was found three proved to be *A. javanicus* and one *A. anomalous*. Since Kniep described both asexual and sexual phases of his Java isolate, however, his species should remain distinct. *A. arbusculus* as here understood is based on Butler's asexual plant and on the strain North Carolina No. 2, whose gametophyte was studied by Hatch. Most of the synonyms are questioned, since they are based on asexual plants alone. Emerson (*loc. cit.*) has fully discussed the relation of *A. Kniepii* to *A. arbusculus*. He also establishes two varieties, based on the differences in size of the resting spores. Since intergrades between them occur he separates them mainly for convenience. In *A. arbusculus* var. *arbusculus* the resting structures average 32–45 μ wide; in var. *minor* they average 24–31 μ wide.

ALLOMYCES JAVANICUS Kniep

Berichte Deutsch. Bot. Gesell., 47:211, figs. 1–7. 1929
(Figure 28 B, p. 400)

Basal cell conspicuous, variable in size, hyphae copiously sympodially or dichotomously branched; zoosporangia ovoid or barrel-shaped, terminal or catenulate, 60–80 μ long by 27–50 μ in diameter, with one or several discharge papillae, zoospores ovoid, 11–12.5 μ long by 8–10 μ in diameter; resting spores ovoid or subspherical,

with rounded apex and truncate base, 34.5–60 μ long by 23.5–35 μ in diameter, the exospore thick, olivaceous brown to tawny or reddish brown,¹ minutely punctate, upon germination forming posteriorly uniflagellate planonts; sexual plant similar to the asexual, gametangia somewhat irregularly arranged, terminal, single, in pairs or catenulate and alternating, the male terminal or, rarely, subterminal, cylindrical, with narrow apex, usually about 34.5 μ long by 23.5 μ broad when terminal, subtended by the somewhat larger, more ovoid female gametangium, which is usually about 51 μ long by 33 μ in diameter, male gamete 4.8–6.3 μ long by 3.4–4.4 μ wide, faintly orange to reddish, female gamete 9–11.5 μ long by 7.5–8.5 μ wide, colorless, the biflagellate planozygote coming to rest to form the new asexual plant.

In soil, Kniep (*loc. cit.*), JAVA; UNITED STATES; MEXICO; TANZANYIKA; BURMA; FIJI.

The description above is based in the main on the Kniep Java No. 1 isolate.

Emerson (1941) describes three varieties of this species: var. *javanicus*, var. *perandrus*, and var. *macrogynus*. The third of these, *Allomyces javanicus* var. *macrogynus* (Emerson & Fox) Emerson, is indistinguishable from Indoh's *A. javanicus* var. *japonensis* (see below). Since a description of Indoh's fungus was published first, Emerson's name lapses into synonymy. The binomial *A. macrogynus* Emerson & Fox (1940) is unaccompanied by sufficient description and is considered a *nomen nudum*.

ALLOMYCES JAVANICUS var. *JAVANICUS* Emerson, Lloydia, 4:132.
1941.

"Gametangia usually rather irregular in shape and arrangement, tending to occur singly or in chains; primary males sometimes hypogynous; females often only slightly longer than males in the primary pairs (averaging about 1.5 times as long as males); females and males usually produced in approximately equal numbers. Female gametes, mean diameter 9–11 μ ; male gametes, 4–5.5 μ . Resistant sporangia formed in abundance or, in certain isolates, sparsely except under adverse conditions; sometimes gray or olivaceous brown; usually with evident pits" (Emerson, *loc. cit.*).

¹ According to Emerson (1941).

ALLOMYCES JAVANICUS var. PERANDRUS Emerson, *Lloydia*, 4:133.
1941.

"As above [var. *javanicus*] but with a great preponderance of male gametangia; about 95% male to 5% female" (Emerson, *loc. cit.*).

ALLOMYCES JAVANICUS var. JAPONENSIS Indoh, Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:265, figs. 1b, 24-28, 29 a-d, 30 a-c. 1940. (Figure 28 C, p. 400.)

Allomyces macrogynus Emerson and Fox, nom. nud., Proc. Royal Soc. London, Ser. B, 128 (852):282. 1940.

Allomyces javanicus var. *macrogynus* (Emerson & Fox) Emerson, *Lloydia*, 4:133. 1941.

"Fungus [in] small white tufts reaching to about 7.5 mm. in length, attached by rhizoids to substrata. Hyphae septated in places by pseudosepta, 30-88 μ thick at base, tapering towards apices, 12-23 μ diam., branched dichotomously or subdichotomously. Sterile branches bluntly pointed. Hyphal membrane does not turn blue with chlor-iodide of zinc. Zoosporangia terminal, sympodially arranged, often secondary sporangia formed next primary ones, from 1 to 5 in chains. Primary ones ovoid, ellipsoid, cylindrical, clavate, 30-56 \times 36-158 μ , average 36.8 \times 110.6 μ , secondary ones barrel-shaped or cylindrical, 20-40 \times 25-150 μ , av. 30.1 \times 68.0 μ . Mature sporangia with apical or lateral from 1 to 3 hemispherical dehiscence papillae, about 5 μ high, 12-14 μ diam. Zoospores amoeboid in emerging state, uniciliate, ovoid, about 8 \times 12 μ in swimming state; after swimming germinate. Chlamydospysts terminal on asexual mycelia, spherical or ovoid, arranged as zoosporangia, appearing salmon-orange color to the unaided eye. Yellowish-brown under microscope, with two layers of membranes, outer one thick, about 1.8 μ in thickness, conspicuously and finely pitted; inner one thin, less than 1 μ in thickness, smooth, escaping from the clasping hyphal membrane or sometimes falling off with membrane. Germination occurs after a rest of several weeks or more. Zoospores from chlamydospysts become sexual mycelia. Sexual reproduction by means of anisogamic gametogamy. Gametangia terminal on sexual mycelia, arranged sympodially, consisting of an apical male gametangium and a basal female gametangium. Often from 2 to 3 pairs of male and

female gametangia arranged in a chain. Male gametangia salmon-orange, globose, $28-40 \mu$ in diam., av. 34μ ; female gametangium grey, cylindrical to barrel-shaped, $40-56 \times 72-120 \mu$, av. $47.5 \times 98.5 \mu$. Ratio of female gametangial length to corresponding male gametangial length 2-3:1. Each gametangium with from 2 to 4 dehiscence papillae. Female gametes subglobose to ellipsoid, $7-10 \mu$ diam., slowly motile, uniciliate; male gametes ellipsoid, $3-4 \times 4-5 \mu$, sluggish motile, also uniciliate. Zygotes motile with two cilia at early stage, losing cilia on coming to rest, then germinating to form asexual mycelia" (Indoh, *loc. cit.*).

In soil, Indoh (*loc. cit.*), JAPAN; coll. W. R. Taylor, isolated F. K. Sparrow, VENEZUELA. (For other isolations see Emerson, 1941.)

SUBGEN. CYSTOGENES

ALLOMYCES MONILIFORMIS Coker and Braxton

J. Elisha Mitchell Sci. Soc., 42:139, pl. 10. 1926. Emend. Emerson, Mycologia, 30:127. 1938
 (Figure 28 F-G, p. 400)

Basal cell up to 150μ or more in length by $17-48 \mu$ in diameter, hyphae tapering, $12-18 \mu$ in diameter, slightly but distinctly constricted at the pseudosepta, dichotomously branched, the pseudocells up to 655μ long, contents in old cultures becoming slightly pink; primary sporangia narrowly clavate or cylindrical, $62-135 \mu$ long by $20-32 \mu$ in greatest diameter, with an apical papilla, secondary sporangia formed predominantly in basipetal succession, ovoid to nearly spherical, with truncate ends and from one to four lateral papillae, successively diminishing in size, the proximal ones as small as 20μ in diameter, contents pink, becoming browner as the zoospores approach maturity; zoospores ovoid, $10-15 \mu$ long by $5-8 \mu$ broad, with a long posterior flagellum; resting spores narrowly to broadly ovoid, with truncate base and pronounced apical beak, usually $43-75 \mu$ long by $21-43 \mu$ in greatest width, generally slipping out of their containers at maturity, the exospore thick-walled, dark orange-brown, with widely spaced pits, germination of the *Cystogenes* type, primary biflagellate planonts and cysts $11-15 \mu$ in diameter, secondary uniflagellate planonts from the cysts $8-9 \mu$ in mean diameter.¹

¹ See the explanation of Figure 29 K-O, p. 404.

In moist sand and loam, Coker and Braxton (*loc. cit.*), UNITED STATES; MEXICO; PUERTO RICO (doubtful); coll. W. R. Taylor, isolated F. K. Sparrow, TRINIDAD; BOLIVIA.

ALLOMYCES NEO-MONILIFORMIS Indoh

Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:270, figs. 2d, 31-33, 34 a-d. 1940

"Fungus rather delicate, tufts mostly 6-7 mm. long, sometimes as much as 9 mm., attached to substrata by well developed rhizoidal systems. Hyphae septated by pseudosepta, subdichotomously branched, from 25 to 43 μ thick at base. Zoosporangia terminal, cymosely arranged, single, clavate to cylindrical or from 2 to 13 catenulate, barrel-shaped, 20-32 \times 66-124 μ , rarely very short, 41-22 μ . Chlamydocysts terminal, cymosely arranged, rarely epigenous on a zoosporangium, globose, ovoid, or elliptical, 30-44 \times 36-64 μ , deciduous and falling from the hyphal membrane. Color of outer membrane of chlamydocyst yellow-ocher, pittings scattered, about 3.5 μ apart. Zoospores discharged from chlamydocysts large, soon encysted, after which several small secondary zoospores swarm out. The small zoospores motile, uniciliate, after germination becoming the usual asexual mycelia" (Indoh, *loc. cit.*).

In soil, JAPAN.

ALLOMYCES CYSTOGENUS Emerson

Lloydia, 4:184, figs. 7, 10A, 15. 1941

(Figure 29 K-O, p. 404; Figure 31, p. 409)

"Characters of the subgenus [*Cystogenes*]. Zoosporangia somewhat elongate, 50-120 \times 20-40 μ ; secondary ones in longer or shorter chains. Zoospores, mean diameter 10-12 μ . Resistant sporangia oval to very elongate and almost clavate but always with broadly rounded apex, 34-95 \times 24-49 μ . Primary R. S. zoospores and cysts quite constant in size; mean diameter 9-12 μ . Secondary R. S. zoospores, mean diameter 6-7 μ . Plants never producing pigment in the cytoplasm as far as known" (Emerson, *loc. cit.*).

BURMA (No. 1 B isolate); CHINA; VENEZUELA; coll. J. V. Harvey, UNITED STATES.

This species closely resembles Indoh's *Allomyces neo-moniliformis*, and a further study may show them to be identical.

ALLOMYCES CYSTOGENUS var. *CYSTOGENUS* Emerson, Lloydia, 4:134. 1941.

"Resistant sporangia oval, less elongate, averaging $51-55 \mu \times 33-38 \mu$; frequently germinating rapidly and with great uniformity as to time of germination and size of cysts produced" (Emerson, *loc. cit.*).

ALLOMYCES CYSTOGENUS var. *ELONGATUS* Emerson, Lloydia, 4:134. 1941.

"Resistant sporangia strikingly more elongate than those of any other form; sometimes clavate; averaging $71 \times 35 \mu$; not usually germinating readily or uniformly" (Emerson, *loc. cit.*).

SUBGEN. BRACHYALLOMYCES

ALLOMYCES ANOMALUS Emerson

Lloydia, 4:133. 1941

(Figure 28 D-E, p. 400)

"Characters of the subgenus [*Brachyallomyces*]. (A problematical subgenus and species tentatively established to include those few isolates in which repeated attempts to obtain sexual plants have been unsuccessful)" (Emerson, *loc. cit.*).

UNITED STATES; MEXICO; INDIA.

BLASTOCLADIA REINSCH

Jahrb. wiss. Bot., 11:298. 1878

(Figure 33, p. 434; Figure 34, p. 438)

Thallus consisting of a cylindrical more or less elongate trunk-like basal cell which is either expanded at its apex or gives rise to broad distally expanded lobes or short clavate branches or to cylindrical slightly tapering dichotomously, subdichotomously, or sympodially arranged branches on which the reproductive organs are borne, septa only delimiting the reproductive organs, the whole anchored to the substratum by a system of branched holdfasts; zoosporangia sessile, with a single apical discharge papilla and, often projecting downward from this, a refractive peglike plug; zoospores posteriorly uniflagellate, with a hyaline often conspicuous subtriangular nuclear cap, formed in the sporangium, after the deliquescence of the papilla

emerging individually or in an evanescent vesicle, the papilla and peg sometimes persistent; resting spore with a thick minutely punctate wall persistent or deciduous, rounded or beaked, with a truncate base, completely filling the thin-walled case in which it is borne, formed on the same or on different plants from the sporangia, upon germination producing planonts; gametophyte apparently not formed.

Saprophytes on decaying twigs and fruits, on which they form crisp hemispherical pustules. Some species may occur alone, but usually they are found growing with other water molds such as *Rhipidium*, *Gonapodya*, and the like. One species, *Blastocladia Pringsheimii*, is undoubtedly extremely common in all fresh-water habitats.

No absolutely conclusive evidence for the occurrence or nonoccurrence in this genus of sexuality or of a gametophyte phase has as yet been presented. This has been due largely to the difficulty in obtaining germination of the resting spores, where, obviously, any significant study should begin. Minden (1916) observed early stages of germination, but evidently did not follow the fate of the swarmers. Miss Blackwell (1937) has secured abundant germination of the resting spores in *Blastocladia Pringsheimii*. The results of her investigations on the further development of the swarmers (Blackwell, 1940) indicate that there is no gametangial plant or alternation of generations in this species. The zoospores from germinating resting spores formed small thalli on which were produced ordinary sporangia and zoospores. The latter were never observed to fuse, but, rather, gave rise to thalli similar to the parent plant. The function, if any, of the sterile setae formed on some plants has not been determined.

Certain species have been carried in pure culture on artificial media, but have not thrived under these conditions, apparently not possessing, as does *Allomyces*, the capacity for unlimited growth of the branches of the basal cell.

The "ramosa" group of *Blastocladia* approximate *Allomyces* in the habit of the thallus. No pseudosepta are formed, however, and the zoospores are discharged through only a single apical papilla.

Identification of the species is complicated by the diverse shapes which the basal apparatus may assume, and in some instances specific characters based on this feature will probably be shown in the future to be of questionable value. In general, however, reliance can be placed on the shapes of the resting spore and the sporangia and, to a lesser degree, on the presence or absence of a distal swelling of the

basal cell or its branches. A study of the variations on different substrata of strains originating from single-spore cultures is greatly needed to clarify specific concepts.

A few studies of the development of the thallus indicate that the holdfast system, which here as in *Allomyces* is considered the homologue of the rhizoids of the chytrids, is derived from the primary germ tube of the zoospore. The basal cell represents the expanded body of the spore itself, and the reproductive organs originate as papilla-like outgrowths from its surface. Although resembling *Rhipidium*, *Mindenella*, and *Araiopora* of the Leptomitales in superficial aspect, exhibiting, in fact, evolutionary parallelism with these genera, *Blastocladia* differs in bearing sessile sporangia, resting spores rather than oöspores, and posteriorly uniflagellate zoospores.

KEY TO THE SPECIES OF BLASTOCLADIA

- Sporangia predominantly cylindrical, at least four times as long as wide; thallus variable in habit
 - Basal cell clavate or globose, with lobes or clavate branches
 - Basal cell distinctly clavate, the branches, when formed, always clavate
 - Sporangia not proliferating *B. Pringsheimii*, p. 431
 - B. aspergilloides*, p. 433
 - Sporangia proliferating *B. Sparrowii*, p. 433
- Basal cell globose, the cylindrical part very short or absent
 - B. globosa*, p. 435
- Basal cell cylindrical throughout, only slightly, if at all, clavate, branched or unbranched
 - Sporangia proliferating *B. prolifera*, p. 436
 - Sporangia not proliferating
 - Sporangia about nine times as long as wide; borne on short branches of the basal cell *B. angusta*, p. 436
 - Sporangia about from three to four times as long as wide; arranged subracemosely, corymbosely, cymosely, or subdichotomously on short branches
 - Sporangia cylindrical to broad-clavate *B. incrassata*, p. 437
 - Sporangia long-cylindrical *B. gracilis*, p. 437
- Sporangia predominantly narrowly or broadly ovoid, fusiform, beaked, or broadly ellipsoidal or dome-shaped and truncate
 - Sporangia narrowly or broadly ovoid or fusiform, appearing beaked; thallus cylindrical throughout

- Walls of the thallus smooth
 Sporangia and the thick-walled brown resting spores appearing beaked *B. rostrata*, p. 439
 Sporangia beaked; resting spores with rounded apex, thin-walled, colorless *B. ramosa*, p. 440
 Walls bearing ridged markings *B. tenuis*, p. 440
 Sporangia broadly ellipsoidal or dome-shaped and truncate
 Sporangia broadly ellipsoidal in dense clusters, basal cell wide, tapering distally, branching apically *B. glomerata*, p. 441
 Sporangia dome-shaped and truncate, few, basal cell cylindrical, only slightly expanded distally *B. truncata*, p. 441

BLASTOCLADIA PRINGSHEIMII Reinsch

Jahrb. wiss. Bot., 11:298. 1878

(Figure 33 D, p. 434)

Basal cell variable in habit and size, generally cylindrical, 400–1000 μ long by 30–90 μ in diameter, wall smooth or rough, up to 8 μ thick, expanded distally and simple or giving rise to cylindrical, apically expanded, subdichotomously, subumbellately, or irregularly arranged branches or broad lobes up to 240–400 μ long by 80–160 μ in diameter, setae present or absent, 2–6 μ in diameter, generally bulbous at the base, holdfasts richly branched, the whole thallus up to 2000 μ long, contents with many globules; sporangia borne along the tips of the branches or over the surface of the swollen lobes, predominantly cylindrical or narrowly clavate, often somewhat curved, also narrowly ellipsoidal, fusiform, long ovoid, or siliquiform, 70–350 μ long by 13–70 μ in diameter, usually at least from three to five or more times as long as broad, the discharge papilla often bearing an endogenous plug, zoospores ovoid and 6–9 μ long by 5–6 μ in diameter, or spherical and 12–15 μ in diameter, emerging individually or in a columnar or pyriform group surrounded by an evanescent vesicle bearing an apical, persistent "plug" (the remains of the discharge papilla), empty sporangia often deciduous; resting spores usually borne among the sporangia, ellipsoidal, ovoidal, or spherical with truncate base, 40–99 μ long by 30–50 μ in diameter, wall thick, brownish, punctate, upon germination the wall splitting and the contents becoming divided into planonts.

Forming dense pustules on apples, Reinsch (*loc. cit.*), fruits and twigs, Minden (1902:823; 1915:603, fig. 13 [p. 580]; 1916:189, 211,

text figs. 15-17, pl. 4, figs. 25-33), substratum (?), Laibach (1927), Behrens (1931), GERMANY; apples and other plant materials, Thaxter (1896a:51, pl. 3, figs. 1-13), fruits of apple, crab apple, rose, *Crataegus*, Kanouse (1927:297, pl. 33, figs. 8-13), apples, Cotner (1930a: figs. 1-4), apples, twigs, Sparrow (1932b:291, pl. 7, fig. H; 1933c:529), UNITED STATES; apples and ash twigs, H. E. Petersen (1909:395; 1910:532, fig. 10), Lund (1934:40, fig. 18), Sparrow, DENMARK; apple, Valkanov (1931a:366), BULGARIA; twigs, Barnes and Melville (1932:94), rose fruits, Cook and Forbes (1933:641), Forbes (1935a:237, pl. 10, fig. 10), twigs and apples, Sparrow (1936a:455, pl. 20, fig. 5), tomato fruits, Blackwell (1937:933; 1940:figs. 1-9), Lloyd (1938:figs. 1-3), ENGLAND; fruits of rose, banana, apples, *Japonica*, winter cherry, *Cotoneaster*, Crooks (1937: 222, fig. 8), AUSTRALIA; *Pirus* fruits, Indoh (1940:250, figs. 9 a-e), JAPAN; apples, Sparrow, HOLLAND.

The commonest species of the genus. As is indicated above, the habit of the plant is extremely variable, and considerable observation on cultures derived from single spore strains growing on various twigs and fruits will be necessary before the species can be adequately delimited. A glance at the figures of what various authors consider this species will show that all plants with somewhat cylindrical sporangia and resting spores which are thick-walled and not beaked have been termed *Blastocladia Pringsheimii*. Certain specimens showing more pronounced variations in thallus habit have been segregated as distinct species (*B. globosa*, *B. aspergilloides*, *B. angusta*, and so on). Attempts have also been made (Lloyd, 1938) to arrange the thallus types in groups, the extremes being on the one hand a globose type with a short cylindrical axis and on the other a slender rameose type. Unfortunately, significant data can only be accumulated by resort to single spore cultures. Lloyd's observations over a period of time on gross cultures of what was considered a single species showed that there was no periodicity in the shape of the thallus, the frequency of resting spores, or the presence or absence of setae. The lobed type with definite cylindrical axis and the branched type with swollen apices predominated. It is important to bear in mind that the latter type was figured by Reinsch as typical of his species.

The sizes given for the thallus are probably of very little significance. Crooks (1937) has determined from a study of the size of the sporangia in 265 individuals that there was wide variation in

this respect, the structures ranging from 70 to 270 μ in length and from 15 to 75 μ in diameter; sporangia 100-210 μ in length by 25-55 μ in diameter were in the majority, whereas those 150-159.9 \times 30-39.9 μ occurred with the greatest frequency.

BLASTOCLADIA ASPERGILLOIDES Crooks

Proc. Roy. Soc. Victoria (N. S.), 49 (2):228, text fig. 11c, pl. 10, figs. 1, 4.
1937

"Plant attached to substratum by means of a few fairly stout rhizoids—up to 5 μ in diameter; plant consists of a single cell, cylindrical in the lower part 25-45 μ in diameter, but expanded at the apex to form a swollen head—60-85 μ in diameter; branched forms were not observed; plants 140-200 μ high, dark in color due to dark brown protoplasm, wall of basal cell fairly thick, 3.5-5 μ ; sterile hairs usually present, only 1-2 μ in diameter; sporangia long, narrow, cylindrical, arising from the swollen head, 85-150 \times 8-15 μ . Zoospores emerge through a terminal opening; resting spores not observed" (Crooks, *loc. cit.*).

On rose hips, apples, AUSTRALIA.

This is only very doubtfully distinct from *Blastocladia Pringsheimii*; it has been seen many times by the author. Generally regarded as a dwarf form of that species, it has in one unusual instance (Sparrow, 1932b:pl. 7, fig. H) been figured attached to a typical plant of *B. Pringsheimii*.

BLASTOCLADIA SPARROWII Indoh

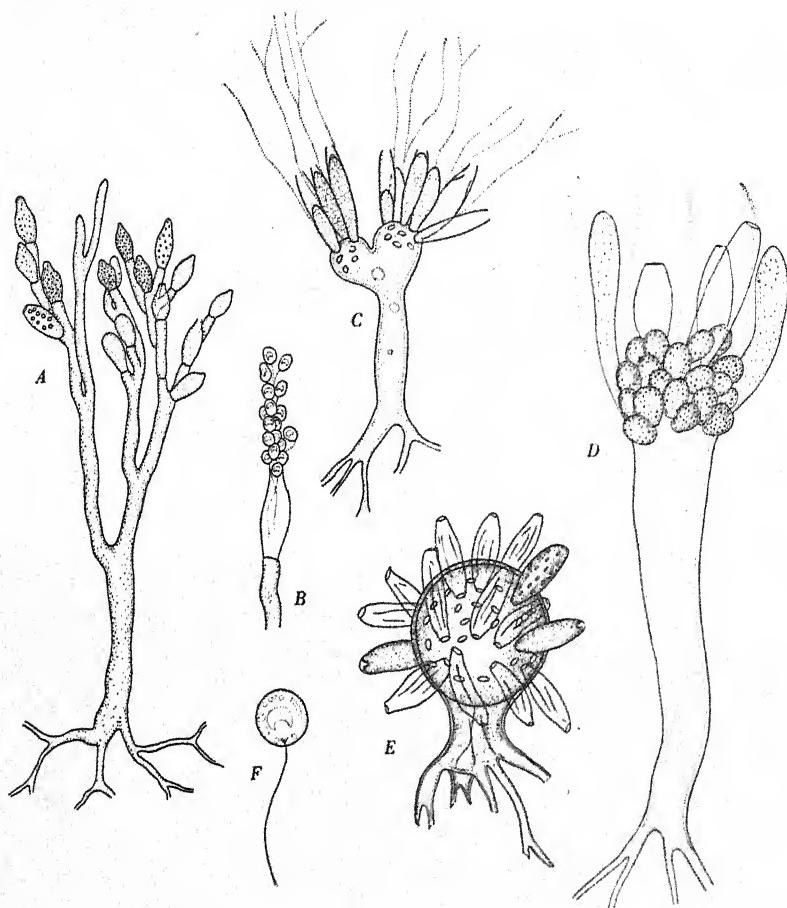
Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:259. 1940
(Figure 83 C, p. 434)

"Basal body cylindrical, 13-31 \times 312-468 μ ; distal portion of basal body greatly swollen, lobed, or more often, unlobed, 47-374 μ in diam., bearing sessile sporangia and sterile setae. Sterile setae branched or unbranched, up to 260 μ long.

"Zoosporangia cylindrical, 13-21 \times 73-143 μ . Internal proliferation of the sporangia frequent and very evident. Zoospores spherical, 5.2 μ diam., posteriorly uniciliate.

"Chlamydospore not observed" (Indoh, *loc. cit.*, modified from Sparrow, 1936a:458, pl. 20, figs. 3, 13).

Saprophytic on twigs of *Fraxinus sp.*, ENGLAND.

FIG. 33. *Blastocladia*

A-B. Blastocladia rostrata Minden: *A*, habit of plant bearing zoosporangia and beaked resting spores; *B*, sporangium discharging its zoospores. *C. Blastocladia Sparrowii* Indoh ($\times 80$), plant bearing setae, proliferated zoosporangia, and lobed basal cell. *D. Blastocladia Pringsheimii* Reinsch ($\times 80$), plant bearing setae, zoosporangia, and resting spores. *E. Blastocladia globosa* Kanouse, plant with spherical basal cell and zoosporangia. *F. Blastocladia* sp., living zoospore, showing internal structure.

(*E*, Kanouse, 1927)

Founded on a fungus identified by Sparrow (*loc. cit.*) as *Blastocladia prolifera* Minden. Because of the apically swollen basal cell and the sterile setae Indoh considers it distinct from Minden's species. In view of the variations found in both the shape of the basal cell and the presence or absence of setae in the closely related *B. Pringsheimii*, the validity of the segregation on these bases may be open to question.

BLASTOCLADIA GLOBOSA Kanouse

Amer. J. Bot., 14:298, pl. 32, figs. 1-4. 1927

(Figure 33 E)

Basal cell globose or subglobose, the proximal cylindrical part very short and 36-60 μ in diameter or absent, distally entire or with large irregular expanded lobes or branches up to 200 μ in diameter by 120-350 μ high, wall thick (up to 10 μ), brittle, laminate, smooth or slightly roughened, contents colorless or brownish, holdfasts stout, much branched, setae present or absent, whole thallus 120-400 μ long and up to 200 μ or more in diameter; sporangia cylindrical or broadly cylindrical, 55-160 μ long by 15-60 μ in diameter, numerous, zoospores posteriorly uniflagellate, spherical or somewhat elongate, 12-14 μ (long?) or 7-9 μ long by 5-6 μ wide; resting spores borne with the sporangia, subspherical, ovoid or subpyriform, with rounded apex and truncate base, 25-70 μ long by 27-50 μ in diameter, wall thick, brownish, punctate, germination not observed.

Forming minute white pustules, particularly on very hard fruits. Fruits of crab apple, *Crataegus*, Kanouse (*loc. cit.*), apples, Cotner (1930a:297, figs. 5-10), Sparrow (1933c:529), UNITED STATES; apple, Sparrow (1936a:458), ENGLAND; fruits of *Solanum pseudo-capsicum*, Crooks (1937:228, text fig. 10 C, pl. 10, fig. 2), AUSTRALIA; fruits of *Cornus officinalis*, Indoh (1940:249, fig. 8), JAPAN.

If, as is possible, this is only a variety of *Blastocladia Pringsheimii*, growing on very hard fruits, it is nonetheless a well-marked and readily identifiable form. As Miss Kanouse points out, the species differs from *B. Pringsheimii* in having a more conspicuously globose basal cell, the cylindrical stalk often being almost entirely absent. When it is present, however, the habit of the plant closely approximates small specimens of *B. Pringsheimii*.

Miss Kanouse describes the zoospores as 12-14 μ in diameter,

kidney-shaped to ovoid when swimming, and biflagellate. Only posteriorly uniflagellate ones have been observed by Cotner (*loc. cit.*) and by Sparrow.

BLASTOCLADIA PROLIFERA Minden

Kryptogamenfl. Mark Brandenburg, 5:606. 1912 (1915); Falck, Mykolog. Untersuch. Berichte, 2 (2):213, text figs. 20-22. 1916

Basal cell cylindrical, 100-300 μ long by 24-80 μ in diameter, apically divided into subdichotomously or irregularly arranged short branches, setae absent, holdfasts branched; primary sporangia numerous, straight-cylindrical or somewhat curved, basally truncate, 60-150 μ long by 13-35 μ in diameter, with a prominent apical papilla, internally proliferous (up to five times), secondary sporangia successively smaller; zoospores spherical, posteriorly uniflagellate, 5.2 μ in diameter; resting spore not observed.

On dead plant parts, Minden (*loc. cit.*), GERMANY; fruits of apple and *Japonica*, Crooks (1937:225, fig. 10 A-B), AUSTRALIA; fruits of *Cornus officinalis* Indoh (1940:254, fig. 11), JAPAN.

Certain plants mentioned by Crooks (*loc. cit.*) may be referable to *Blastocladia Sparrowii*.

BLASTOCLADIA ANGUSTA Lund

Kgl. Danske Vidensk. Selsk. Skrift., Naturv. Math., Afd. IX, 6 (1):44, fig. 21. 1934

(Figure 34 F, p. 438)

Basal cell cylindrical, slender, up to 150 μ long by 10-35 μ in diameter, the distal part branched (occasionally unbranched), the branches remaining cylindrical, holdfasts slender, branched, whole thallus 160-500 μ long, contents sometimes brownish, setae usually present; sporangia borne at the tips of the branches, narrowly cylindrical, 60-210 μ long by 6-25 μ in diameter; zoospores not observed (?), apparently liberated through an apical pore; resting spore broadly ovoid and beaked, base narrow and truncate, 25-45 μ long by 16-26 μ wide, wall thin, colorless, possibly pitted on inner face, germination not observed.

Forming small whitish pustules. On apple fruits, Lund (*loc. cit.*), DENMARK; rose fruits, Crooks (1937:227, text fig. 11 D-G, pl. 10, fig. 5), AUSTRALIA.

The resting spores found by Crooks resemble in shape those of *Blastocladia rostrata*, but if these were actually mature specimens the wall is much like that of the resting structures of *B. ramosa*.

BLASTOCLADIA INCRASSATA Indoh

Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:252, text fig. 10. 1940
(Figure 34 E, p. 438)

"Fungus-colony small, white, in compact tufts; basal body cylindrical, rather broad at upper end, closely branched in dichotomous or racemose manner, at lower end attached by scanty rhizoids. Whole fungus 200–500 μ high, 15–50 μ diam. at base. Cell wall smooth, hyaline, thin, about 2 μ thick. Plasm granulous with oil drops.

"Zoosporangia terminal on branches, sessile, single, racemosely or cymosely arranged, cylindrical to broad clavate, 18–28 \times 50–88 μ , with truncate base, having apically a single dehiscence papilla about 3 μ high.

"Chlamydospyst not observed" (Indoh, *loc. cit.*).

On submerged fruits of *Cornus officinalis*, Indoh (*loc. cit.*), JAPAN; Minden (1916: pl. 4, fig. 26), GERMANY; Sparrow (1936a:455, pl. 20, fig. 7), ENGLAND.

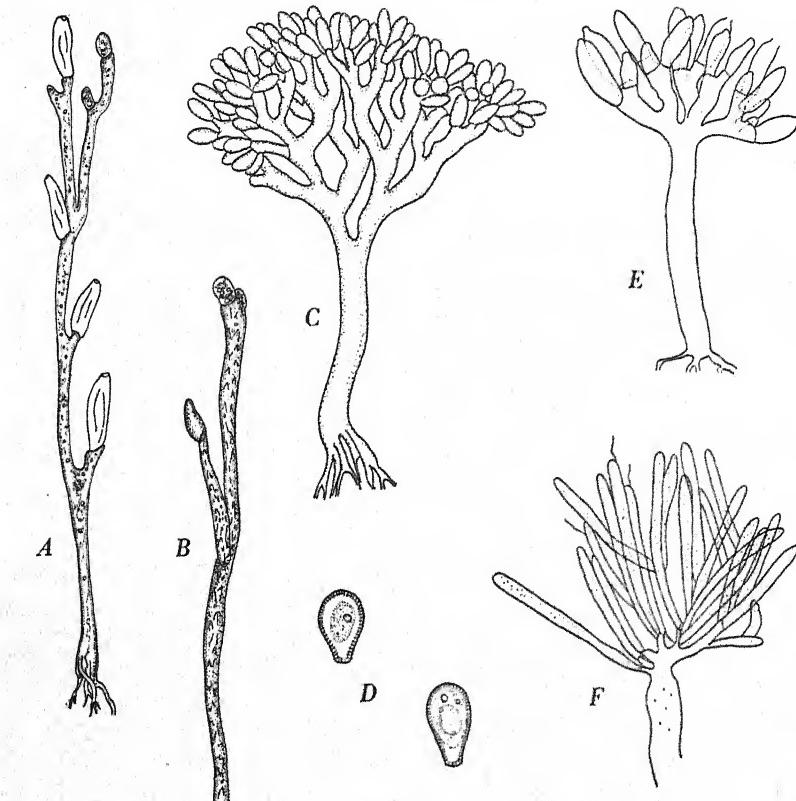
Erected to include certain forms of *Blastocladia Pringsheimii* described by Minden, the organism identified by Sparrow as *B. ramosa*, and the Japanese fungus. Doubtfully distinct from *B. gracilis*.

BLASTOCLADIA GRACILIS Kanouse

Amer. J. Bot., 14:300, pl. 33, figs. 14–16. 1927
(Figure 34 A, p. 438)

Blastocladia ramosa var. *luxurians* Kanouse, Papers Mich. Acad. Arts, Sci., Letters, 5:113, pl. 1, fig. 1. 1926.

Basal cell slender, 20–80 μ in diameter, cylindrical throughout, distally racemosely or subdichotomously branched, walls 2.5–4 μ thick, smooth, contents colorless, setae present or absent, holdfasts few, poorly developed, whole thallus 600–950 μ long; sporangia racemosely or corymbosely arranged along the branches, long-cylindrical, 70–220 μ long by 20–34 μ in diameter, with a prominent discharge papilla; zoospores (?) apparently escaping through an apical pore; resting spores borne with the sporangia, usually terminal,

FIG. 34. *Blastocladia*

A. *Blastocladia gracilis* Kanouse, habit of plant bearing racemously arranged empty zoosporangia. B. *Blastocladia tenuis* Kanouse, plant showing sculptured wall. C-D. *Blastocladia ramosa* Thaxter: C, habit of plant ($\times 75$); D, optical-section views of two resting spores ($\times 500$) from type material, showing canals of pits in outer walls. E. *Blastocladia incrassata* Indoh ($\times 100$), habit of plant. F. *Blastocladia angusta* Lund ($\times 129$), habit of upper part of plant.

(A, Kanouse, 1927; B, after Kanouse, 1927; C, after Thaxter, 1896a; E, Indoh, 1940; F, Lund, 1934)

ovoid, subspherical or spherical with truncate base, $40-66 \mu$ long by $20-40 \mu$ in diameter, wall thick, brownish (?), punctate, germination not observed.

In loose tufts or mats with other water molds, particularly *Blastocladia Pringsheimii* and *Rhipidium*. On fruits of apple, Kanouse (*loc. cit.*), UNITED STATES; apples, Lund (1934:43, fig. 20 a-b), DENMARK; apples, rose fruits, Crooks (1937:226, fig. 11 A-B), AUSTRALIA.

Whether or not this is a form of *Blastocladia Pringsheimii* is open to question. Plants of that species when growing in dense stands in long slits on apple fruits frequently assume the habit of *B. gracilis*.

BLASTOCLADIA ROSTRATA Minden

Kryptogamenfl. Mark Brandenburg, 5:604. 1912 (1915); Falck, Mykolog. Untersuch. Berichte, 2:211, text figs. 18-19, pl. 4, figs. 34-35. 1916
(Figure 33 A-B, p. 434)

Basal cell narrowly or broadly and irregularly cylindrical, 140-150 μ long by 15-63 μ in diameter, profusely branched and rebranched dichotomously, pseudodichotomously, or sympodially, remaining cylindrical throughout, holdfasts stout, branched, setae absent, entire thallus 500-1500 μ long; sporangia spirally arranged, terminal or intercalary and sessile or on short lateral branches, cylindrical, subcylindrical, predominantly distinctly long-fusiform, basally truncate, with a prominent apical papilla, 45-100 μ long by 17-40 μ in greatest diameter; zoospores spherical or slightly elongate, posteriorly uniflagellate, 7.5-10 μ in diameter, emerging in a compact column before dispersal; resting spores broadly fusiform or ellipsoidal, with a pronounced apical beak and a truncate slightly elongate base, 30-53 μ long by 15-30 μ in greatest diameter, contents with globules, wall moderately thick, brown, punctate, occurring alone or with the sporangia, at maturity falling out of the thin-walled enveloping case, germination not observed.

Forming a fairly loose turf on the surface of the substratum or mixed in pustules with other water molds. On fruits, Minden (*loc. cit.*), GERMANY; twigs of *Aesculus*, Lund (1934:42, fig. 19), DENMARK; twigs of *Aesculus sp.*, Sparrow (S.) (1936a:455, pl. 20, fig. 14), ENGLAND.

No resting spores were observed in the Danish material reported by Lund.

BLASTOCLADIA RAMOSA Thaxter

Bot. Gaz., 21:50, pl. 3, figs. 14-16. 1896

(Figure 34 C-D, p. 438)

Basal cell cylindrical, up to 400μ long by $14-25 \mu$ in diameter, divided distally dichotomously or subdichotomously into from two to several secondary slightly tapering axes which branch and rebranch sympodially or somewhat irregularly, holdfasts delicate, sparingly branched, wall thin, smooth, setae absent, whole thallus delicate, with an open rameose habit, up to $260-1000 \mu$ high; sporangia terminal and subterminal, on short branches, either narrowly or broadly ovoid with a narrow truncate base or broadly fusiform, $30-41 \mu$ long by $7-15 \mu$ in diameter, papilla apical; zoospores ellipsoid to pyriform, $5-6 \times 6-7 \mu$, posteriorly uniflagellate; resting spores borne like the sporangia, broadly ovoid, narrowly clavate or spatulate, with a rounded apex and a narrower truncate base, $18-30 \mu$ long by $11-15 \mu$ in diameter, wall colorless or faintly brown, slightly thickened, minutely punctate, germination not observed.

Among other water molds or forming minute pustules. On twigs, Thaxter (F.) (*loc. cit.*), twigs of *Populus trichocarpa*, Graff (1928:169), apple, Sparrow (S.) (1932b:293, pl. 8, fig. J), UNITED STATES; fruits, Minden (1915:605; 1916:197, pl. 4, figs. 36-37), GERMANY; fruits of banana, Crooks (1937:226, fig. 11 H-I), AUSTRALIA; *Pirus* fruits, Indoh (1940:250, fig. 9 a-e), JAPAN.

In its general aspect the thallus of this species resembles *Allomyces*. Study of the resting spores of the type material shows them to be faintly brownish and minutely punctate (Fig. 34 D).

BLASTOCLADIA TENUIS Kanouse

Amer. J. Bot., 14:301, pl. 33, figs. 5-7. 1927

(Figure 34 B, p. 438)

Basal cell narrowly cylindrical throughout, if at all branched then only once or twice near the middle, $300-1000 \mu$ long by $30-60 \mu$ in diameter, wall thin ($3-4 \mu$), golden brown, very brittle, sculptured throughout with ridged markings, setae absent, holdfasts delicate, few, branched; sporangia few, terminal at the apices of the basal cell or its branches, somewhat fusiform with beaklike apex, 27μ long by 11μ in diameter; zoospores not observed; "oögonia" borne

singly or in clusters at the apex of the basal cell, irregularly pyriform or broadly dome-shaped, mature resting spore not observed. (Modified from Kanouse.)

Forming tufts on fruits of rose and *Crataegus* in stagnant water,
UNITED STATES.

Although the character of its wall distinguishes this species from others of the genus further observations are needed on the reproductive organs.

BLASTOCLADIA GLOMERATA Sparrow

J. Linn. Soc. London (Bot.), 50:456, text fig. 5 f-j, pl. 20, figs. 4, 9. 1936

Basal cell stout, very broad at the base, often strongly tapering, 312–364 μ long by 104–162 μ in diameter, rarely unbranched, usually giving rise distally to from two to six broad somewhat clavate branches 195–556 μ long by 52–111 μ in diameter, setae branched or unbranched, holdfasts stout, branched, whole thallus exclusive of holdfasts and setae 693–1020 μ long; sporangia occurring in dense clusters at the tips of the branches, predominantly broadly ellipsoidal, often slightly curved, resting on a truncate, collar-like base, 63–169 μ long (majority 88–100 μ) by 34–63 μ in diameter (majority 42–52 μ), ratio of length to width 1.3–2.3:1; zoospores spherical, 10 μ in diameter, posteriorly uniflagellate; resting spores borne among the sporangia, nearly spherical, ovoid or somewhat elongate, basally truncate, 39–52 μ long by 36–49 μ in diameter (average 46 \times 39.6 μ), wall thick, punctate, dark brown, germination not observed.

Forming large coarsely granulated pustules on twigs of *Aesculus* sp., Sparrow (S., B. M.), ENGLAND.

Certain forms of *Blastocladia Pringsheimii* figured by Minden (1916:fig. 15) and Lund (1934: fig. 18b) resemble *B. glomerata* to a degree. Though its resting spore is practically identical with that of *B. Pringsheimii*, *B. glomerata* differs from this species in the shape of the basal cell and more especially in the ratio of length to width of the sporangia (1.3–2.3:1 as compared to 6.4–8:1).

BLASTOCLADIA TRUNCATA Sparrow

Mycologia, 24:293, pl. 7, fig. G. 1932

Basal cell narrowly cylindrical, unbranched, slightly expanded at the apex, 250–286 μ long by 7.7–26 μ in diameter; setae lacking.

holdfasts slightly branched; sporangia borne on the apex of the basal cell, truncate, nearly as broad as long, $10.4-15 \mu$ long by $10.4-12 \mu$ in diameter, appearing more acuminate after discharge; zoospores spherical, 3.5μ in diameter; resting spore not observed.

Forming pustules with other water molds on fruits of apple,
UNITED STATES.

Although this species does not appear to be simply a form of *Blastocladia Pringsheimii*, further observations on it and particularly on the character of the resting spores would be desirable.

IMPERFECTLY KNOWN SPECIES OF BLASTOCLADIA

? BLASTOCLADIA SP. Indoh

Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:259. 1940

"Fungus-body arbuscule, consisting of broad cylindrical trunk-like basal body and thin, well ramified branches, $700-800 \mu$ high. Basal body $60-100 \times 400-700 \mu$, attached to substrata by means of sparsely branched rhizoids, branches dichotomous to irregular, $20-25 \mu$ diam.

"Zoosporangia (?) terminal, sympodially arranged on the branches, cylindrical, $19-20 \times 22-30 \mu$, with a single dehiscence papilla, apically. Zoospores not observed.

"Chlamydocysts sympodially arranged on the branches, elliptical to pyriform, $40-47 \times 45-85 \mu$, with attenuated base, yellowish, containing many oil drops; two membraned, the outer conspicuously pitted. Spore-dehiscence not observed" (Indoh, *loc. cit.*).

Saprophytic on submerged twigs of *Morus sp.*, JAPAN.

Indoh considers this incompletely observed fungus to be most closely related to *Blastocladia gracilis* and *B. incrassata* but different from them in that "(1) the basal body is thicker than that of *Bl. gracilis* and longer than that of *Bl. incrassata*, (2) the zoosporangia (?) are shorter than those of the two, (3) the chlamydocysts are longer than those of *Bl. gracilis*, and not truncated, but somewhat attenuated basally."

MONOBLEPHARIDALES

IN 1871 Cornu published his discovery of a new genus of aquatic fungi which, in contrast to all other known forms, possessed motile sperms. Three species, *Monoblepharis (Gonapodya) prolifera*, *M. sphaerica*, and *M. polymorpha*, were briefly characterized at that time. The following year, in his classic *Monographie des Saprolegniées* (1872a), he described the last two fungi more completely and illustrated them; he also included a brief description, without figures, of the first, *M. prolifera*. This species he figured two years later in the 1874 edition of van Tieghem's *Traité de Botanique* (French edition of Sachs's *Lehrbuch*).

Many years elapsed before any members of the genus were again observed. Indeed, as Thaxter (1895a), presumably the second person to find these organisms, suggested (1903), mycologists were doubtful whether or not a group of fungi with such unique characters actually existed. With the appearance of Thaxter's paper in 1895 all doubts were dispersed, and information concerning the genus *Monoblepharis* was considerably increased. Further investigations, especially those of Lagerheim (1900) in Sweden and Woronin (1904) in Finland, have greatly extended this knowledge, as has the more recent work in Germany by Laibach (1926, 1927) on the cytological aspects of the group.

Monoblepharis was regarded by Cornu as a member of the Saprolegniaceae. It was placed in a separate family, the Monoblepharidaceae, by Fischer (1892). Schroeter (1893), Minden (1915), and later authors have segregated the genus in a distinct order, the Monoblepharidales. As has been pointed out by the author (1933b), this order is closely related to the Blastocladiales.

In 1939 a member of this order (*Monoblepharella Taylori*) with a most curious type of sexual reproduction was discovered in soils from tropical America (Sparrow, 1939d, 1940b). The fungus not only formed motile zoospores and antherozoids, but the zygote as well was free-swimming. Further remarkable features were the occasional formation of more than one egg in the oögonium and the fact that the zygote was propelled by the persistent flagellum of the male gamete.

Most members of the order may be obtained from a single favorable situation. The supposed rarity of these forms appears due largely to lack of information concerning proper methods of collection and of subsequent treatment of material.

(Species of *Monoblepharis* are primarily inhabitants of dead, entirely submerged twigs in permanent fresh-water habitats.) In the collection of such twigs several factors should be borne in mind. First, the pool must be relatively quiet and free from silt and from an excess of products of organic decomposition. Secondly, the twigs must not be decorticated and should preferably be waterlogged. Thirdly, certain twigs, notably those of birch and ash, seem particularly suited to the requirements of the fungus.

Other types of substrata, such as animal cadavers (insects?), twigs of other broad-leaved trees, needles, twigs, and sap of coniferous trees, submerged lichens and fungi, and fruits, have also been described as favorable to the development of *Monoblepharis*.

Material of the fungus seems to be rarely found on twigs brought in from the field and immediately subjected to examination. If, however, such twigs are placed in sterile distilled water and maintained at 8-15° C. for from three to seven days, the fungus, if it is present on the substratum, will often by then have produced an abundance of growth. In such cases there will appear tufts or pustules of very delicate pale-gray rather flexuous hyphae, which may cover the twig or be confined to the openings of the lenticels. If, subsequently, material thus obtained is maintained at 8-11° C. only sporangia will develop, whereas if the same culture is placed at room temperature (21° C.) sexual reproduction will ensue.

Monoblepharella has thus far only been recovered from wet soil in water cultures baited with vegetable material.

Species of *Gonapodya* are frequently found on twigs along with *Monoblepharis*. They are much more common on submerged fruits, however, particularly on those of apple and rose. On these substrata the fungus will form a loose filmy mass, or, more frequently, it will occur in definite pustules on the surface of the fruit in association with *Blastocladia* and *Rhipidium*. The surest method of obtaining such fruit-inhabiting fungi is to construct traps of galvanized wire screening, place the fruits inside, and submerge them in some likely aquatic habitat. Such traps when left for at least a month will usually yield an abundance of material of *Gonapodya* and other

Phycomycetes. After examination the fruits may be placed in jars with a relatively large amount of water, left at a low temperature ($3\text{--}8^\circ\text{ C.}$), and examined at intervals. Further details of these culture methods may be found in papers by Kanouse (1926, 1927).

DEVELOPMENT AND MORPHOLOGY THE THALLUS

Since more is known about the development of *Monoblepharis* than about that of any other member of the order, it will be considered here in detail.

The zoospore of *Monoblepharis* upon germination may produce two germ tubes, one giving rise to the holdfast system which anchors the plant to the substratum, the other producing the main body of the plant. According to Lagerheim (1900), holdfasts may also be formed by the ramifying hyphae.

Once the fungus is established there results, under favorable conditions, an abundant mycelial growth, the nature and extent of which appear to depend somewhat on the particular species. For example, in *Monoblepharis macandra* the growth and branching may be exceedingly profuse and may result in a solid mat of interlocking tangled hyphae covering the substratum, whereas in the other species the filaments seem more rigid and less branched, and tend to remain separated from one another. The finely granular content of the hyphae, in which are occasional refractive granules, is usually disposed, because of the regularly placed vacuoles, in a reticulate or foamy manner. The striking effect produced by this type of vacuolization makes it comparatively easy for one to recognize, even in the vegetative state, a member of the Monoblepharidales. Under changing environmental conditions the protoplasm may temporarily assume a nonvacuolate homogeneous texture.

The thallus and sporangia of *Monoblepharella Taylori* resemble in superficial aspect those of *Monoblepharis regnans* and *M. ovigera*. The mycelium, which forms a lustrous pearly-gray halo around the substratum, is composed of delicate moderately branched hyphae $2\text{--}3\ \mu$ in diameter. Near the base, where the plant is anchored by a system of holdfasts to the substratum, the hyphal axes may attain a diameter of $5\ \mu$. Catenulate series of swellings are formed on the hyphae of some, but not of all, isolates. It is suspected that these are due to an extraneous parasitic organism, but no reproductive

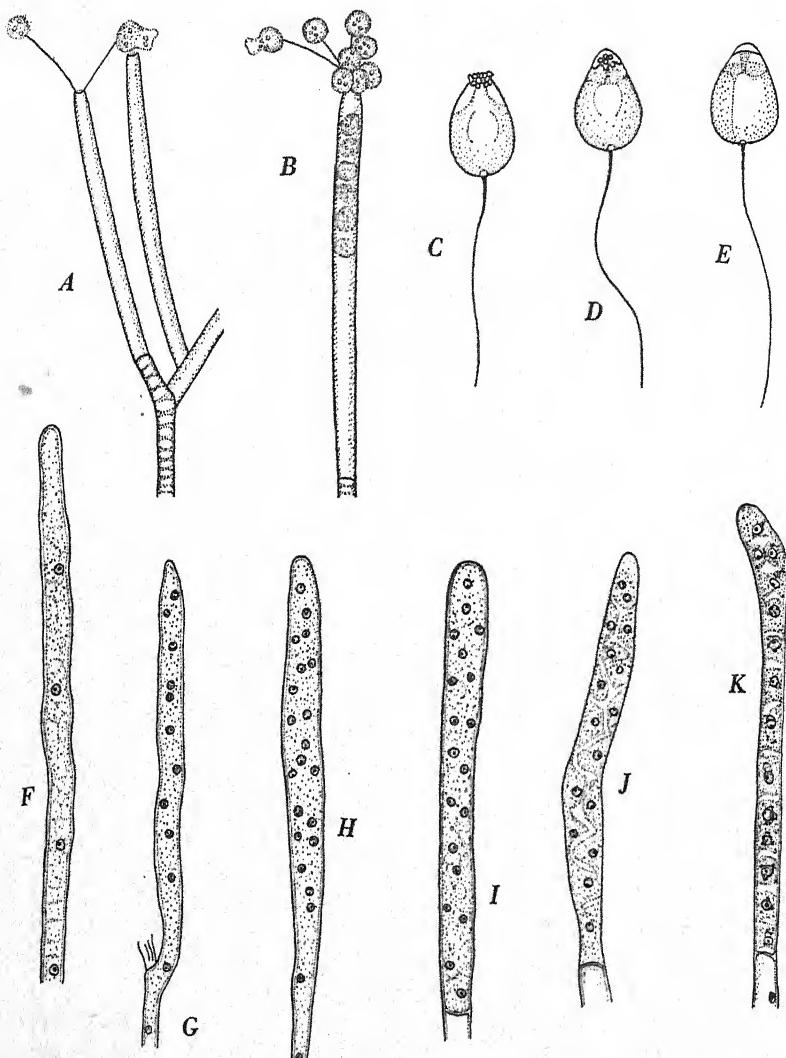


FIG. 35. Nonsexual reproduction in *Monoblepharis*

A-B. Discharging zoosporangia of *Monoblepharis macrandra* (Lagerheim) Woronin ($\times 375$). C-E. Freehand drawings of moving zoospores of *Monoblepharis polymorpha* Cornu, showing internal structure. F-K. Cytoplasmic preparations of developing sporangia in *Monoblepharis macrandra*

phase has ever been observed which would substantiate this idea. The contents are characteristically disposed in a rich network or reticulum, within which may be seen, moving along the long axis of the hypha, somewhat coarse refractive granules of irregular size. A preliminary cytological examination of these hyphae show the minute nuclei to be disposed at more or less uniform intervals.

REPRODUCTION

Nonsexual Reproduction

In most species of *Monolepharis*, at about 8–11° C., only nonsexual reproductive organs are formed. These are usually terminal, slightly swollen, cylindrical portions of the hyphae, with homogeneous contents. Each sporangium is finally separated by a cross wall from its adjacent hypha. According to Laibach (1927), the nuclei are at first more or less regularly placed in the hyphae (Fig. 35 F). As the rudiment of the sporangium begins to form there is an increase in the number of nuclei in that body (Fig. 35 G–H). No mitotic figures were observed in the process of sporangial formation by either Lagerheim (1900) or Laibach. It remains a question, therefore, whether this increase is due to a migration into the sporangium or to the division of a few nuclei. As the cross wall is laid down the nuclei become more or less equidistant from one another (Fig. 35 I). A central vacuole appears during differentiation of the zoospores (Fig. 35 J). Coincident with spore cleavage there is a marked increase in the size of the individual nucleus, which now exhibits around its periphery masses of dark-staining material. Laibach suggests that this material may be connected with flagella formation.

The cleavage planes of the spores appear in most instances to be at right angles to the long axis of the sporangium, although many may be obliquely placed (Fig. 35 K). The spore initials are at

(Lagerheim) Woronin ($\times 440$): *F*, tip of hypha before initiation of sporangium formation; *G–H*, young sporangia before formation of basal cross walls; nuclei have increased in number and some are paired, possibly as a result of a recent division; *I*, sporangium with basal cross wall laid down, separating it from hypha; nuclei are more regularly distributed in cytoplasm; *J*, vacuole formation delimiting spore initials; *K*, further differentiation of zoospores; dark-staining material is present in cytoplasm in vicinity of nuclei.

(*A–E*, Sparrow, 1933b; *F–K*, Laibach, 1927)

first angular in outline, but gradually become more rounded. During this process of cleavage all the protoplasm may not be used up in the formation of the spores, and small bits may remain in the sporangium after discharge. By the deliquescence of the tapering apex of the sporangium a circular, sometimes angular, pore is formed, through which the swarmers creep in amoeboid fashion to the outside medium. There the zoospore remains adherent by its flagellum to the mouth of the sporangium for a varying length of time and may oscillate for some little while before finally becoming disengaged. In the meantime other spores may continue to emerge, and it is not uncommon to see three or more thus attached to the orifice of the sporangium (Fig. 35 A-B). The zoospore at this stage exhibits an almost homogeneous content, in which are imbedded a few refractive granules. Ultimately, by a quick succession of vigorous jerks it becomes entirely free from the sporangium, and either immediately darts away or floats for a time, feebly lashing its flagellum. The latter, which is about four or five times the length of the diameter of the spore body, slowly increases its rate of vibration and, trailing behind, propels the spore in a smooth gliding lively fashion through the water. After complete discharge of the zoospores further sporangia may be formed by cymose branching of the hypha or, in *Monoblepharis regnans* and occasionally in *M. sphaerica* and *M. ovigera*, by proliferation through the empty sporangium.

Recently discharged zoospores undergo a remarkable transformation, for the internal structure, at first nearly homogeneous, assumes such a definite, characteristic arrangement that it enables one to recognize free-swimming spores of this genus, as well as those of *Monoblepharella* and *Gonapodya*. When the spore is in motion, however, the refractive granules previously mentioned come to occupy the most distal portion of the now more cylindrical spore body, and, indeed, often appear to protrude from the somewhat acuminate slightly quivering apex (Fig. 35 C, p. 446). Sometimes they seem to be fused into a single broadly conelike structure (Fig. 35 D-E). Immediately beneath them is a space entirely devoid of granular material. A narrow band or strand connects the granules with the rest of the spore body or possibly with the nucleus. The greater part of the spore is of a very finely granular slightly refractive protoplasm, which appears in some views to be a band the two ends of which have fused (Fig. 35 E). At the point of insertion of the flagellum a highly refractive body may usually be

found. The little-known figures of zoospores and antherozoids given by Cornu in van Tieghem's *Traité de Botanique* indicate that he was well aware of this characteristic internal structure. It is essentially like that observed in the swarmers of *Blastocladia*, *Allomyces*, and such chytrids as *Nowakowskella* and *Cladochytrium*, although *Blastocladia* and *Allomyces* lack the well-organized nearly centric globule found in the other two genera.

In *Monoblepharella* nonsexual and sexual reproductive organs may occasionally be formed simultaneously on the same plant. At room temperature (20–21° C.), however, a preponderance of zoosporangia are produced, whereas at 30° C. sexual organs occur in abundance.

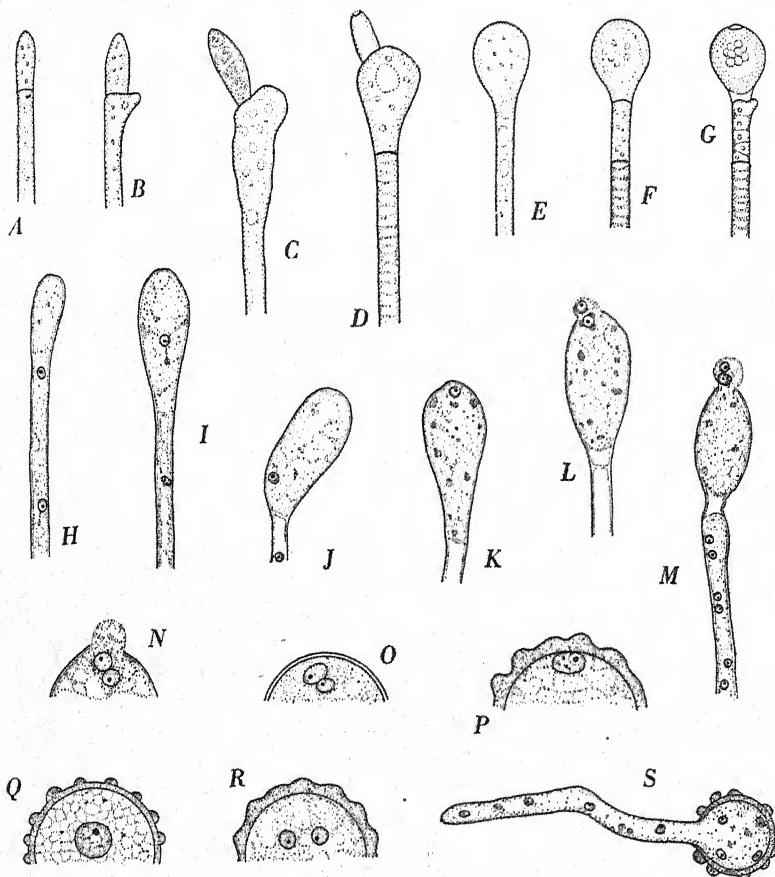
The zoosporangia are ordinarily formed at the periphery of the colony, at the tips of delicate, sparingly branched hyphae. By subsequent sympodial branching of the hypha they appear lateral. The difference in width of the sporangium and its attendant hypha is so striking that the sporangia frequently resemble long slender fusiform or siliquiform highly refractive conidia lying free in the tangled mycelial complex. The zoospores are fully matured before discharge, and emerge through a small pore formed upon the deliquescence of the sporangial apex, in the same manner as in species of *Monoblepharis*. They are ovoid or somewhat cylindrical, and have a single long posterior flagellum. The internal organization is exactly like that in *Monoblepharis*.

It can reasonably be supposed that the development of the sporangial plant of *Gonapodya* and its method of anchorage are essentially similar to those of *Monoblepharis*. Further study of these processes, however, and especially of the origin of the pseudosepta, is greatly needed. In its cytological aspects the sporangium of *Gonapodya prolifera* (Laibach, 1927) resembles that of *Monoblepharis*. As has been pointed out previously, the type of zoospore and method of formation are also similar to those of *Monoblepharis*.

Sexual Reproduction

The extraordinary type of sexual reproduction found among members of this order has made the group one of greatest interest to the mycologist as well as a never-failing source of stimulation to the student of phylogeny.

Details of the sexual reproduction of *Monoblepharis* were accurately portrayed by Cornu, and the observations of the few subsequent workers have added little except cytological data. In

FIG. 36. Sexual reproduction in *Monoblepharis*

A-D. Method of development of sex organs in *Monoblepharis polymorpha* Cornu ($\times 375$): A, terminal antheridium cut off by basal cross wall; B, same, showing beginning of formation of oögonial rudiment beneath antheridium; C, further expansion of oögonial rudiment; antherozoids have matured and are about to be discharged; D, nearly mature oögonium, now separated by basal cross wall from hypha; antherozoids have been discharged from antheridium, which appears to be placed on oögonium. E-G. Method of development of sex organs in *Monoblepharis sphaerica* Cornu ($\times 375$): E, oögonial rudiment forming terminally on hypha; F, nearly mature oögonium cut off by basal cross wall; a cylindrical section immediately beneath, the antheridial rudiment, has been delimited; G, mature oögonium and

Monoblepharis polymorpha, *M. fasciculata*, and *M. insignis* the antheridia appear at first glance to be inserted on the oögonia (epigynous). A study of their development, however, indicates that the oögonium is formed beneath the antheridium and is an intercalary structure. In such a typical epigynous form as *M. polymorpha* the antheridium originates as a walled-off terminal portion of the hypha, the contents of which are rather homogeneous (Fig. 36 A). The more proximal portion of the hypha just beneath the antheridial cross wall then gradually becomes distended and forms a lateral somewhat oblique projection (Fig. 36 B). This lateral distention continues, and a clavate body eventually separated from the hypha by a basal cross wall is formed (Fig. 36 C-D). Often, before the formation of the septa, the antheridium has discharged its antherozoids. The oögonium thus delimited gradually becomes more rotund (Fig. 36 D).

Monoblepharis sphaerica and *M. macrandra*, though having essentially the same type of sex organs as does *M. polymorpha*, differ from it in their methods of development.

In *Monoblepharis sphaerica* the oögonial rudiment is formed first in a terminal position (Fig. 36 E). After the oögonium is delimited another more proximal hyphal segment is blocked off, which becomes the hypogynous antheridium (Fig. 36 F). Within it, sperms are formed (Fig. 36 G) which escape in the usual manner from a

antheridium. H-S. Cytological preparations of developing oögonia, fertilization process, and formation and germination of oöspores of *Monoblepharis macrandra* (Lagerheim) Woronin (all?) (H-M, S, $\times 440$; N-R, $\times 825$): H-I, beginning of formation of oögonium; single egg nucleus is already clearly distinguishable; J, oögonium delimited by cross wall; enlarged nucleus has not as yet migrated to apex of oögonium; K, mature oögonium with apical nucleus; L, mature egg in act of being fertilized by antherozoid; nuclei of the two gametes are clearly visible; deeper-stained areas may be seen in oöplasm, as in preceding figure; M, beginning of emergence of zygote from oögonium; the two nuclei lie in close proximity but are not as yet fused; N, the two nuclei lying side by side in fertilized egg; O, portion of young oöspore before fusion of nuclei; P, old oöspore with single diploid nucleus; Q, oöspore after winter rest period with resting diploid nucleus; R, binucleate stage previous to germination; S, germinated oöspore with multinucleate germ tube.

(A-G, Sparrow, 1933b; H-S, Laibach, 1927)

slightly exserted tubelike outgrowth immediately below the oögonial septa. In *M. macrandra* the antheridia and oögonia first formed are produced terminally on different hyphal branches (Fig. 39 E, p. 466). As growth and reproduction proceed the dichlinous habit is lost, and oögonia and antheridia occur in various positions. If both organs are formed on a single hyphal branch, however, alternating groups of one or the other type of structure are generally developed.

Maturation and escape of the antherozoids are accomplished in the manner described for the zoospores. The antheridia, however, in contrast to the sporangia, bear relatively few motile bodies (from four to eight). In their shape, internal structure, and flagellation, these resemble zoospores (Fig. 37 G, p. 454). They are smaller, however, and, unlike the zoospores, exhibit a pronounced tendency toward amoeboid movement.

Further maturation of the oögonium involves the formation of a highly refractive apical receptive papilla (Fig. 37 A, p. 454). Coincident with, or often before, the formation of this structure the minute evenly disposed oil droplets in the oöplasm combine to form a number of large refractive globules. These, as the ripening of the egg progresses, may come to occupy a central position in the oögonium. Both Lagerheim and Laibach have shown that the egg is uninucleate, and that the nucleus ultimately attains a terminal position in the oögonium (Fig. 36 H-K, p. 450).

Apparently fertilization is possible only after the egg has reached the proper stage of development. It was frequently observed that antherozoids creeping over immature eggs could not fertilize them. Often, too, they seemed unable to fertilize ova which, by their appearance, were fully mature. Whether this was due to the fact that the eggs were only seemingly mature or to the circumstance that the antherozoids from androgynous antheridia were unable to fertilize their own oosphere is in need of further investigation. The latter explanation does not seem to suffice in all instances, however, for numerous examples of self-fertilization may be found.

When an antherozoid approaches the apex of an oögonium the peripheral collar of the wall of the latter, until then contiguous with the papilla (Fig. 37 B, p. 454), dilates slightly (Fig. 37 C-D). The sperm resting on the papilla, which seems to be an integral part of the oöplasm, is immediately engulfed (Fig. 37 E-F), and both sperm and papilla become relatively indistinguishable from the egg. The

flagellum of the sperm may protrude for a few moments, but it, too, is finally absorbed. After fertilization, the egg, which has previously become more compact and has moved toward the apex of the oögonium, retreats slightly and remains motionless for from three to five minutes. It then expands, and there is initiated a gradual evacuation from the oögonium (Fig. 37 H-J). The time required for this process varies, but it usually takes at least two minutes. The wall of the oögonium is again dilated as the egg commences to emerge. In rare instances the protoplasm of the antherozoid may still be distinguishable at this time.

Outside, the egg remains attached by a narrow hyaline collar to the mouth of the oögonium. A pellicle soon forms around it, which gradually thickens and on which there appear regularly placed protuberances (Fig. 37 J-K, p. 454). The latter grow in size and become the bullations so characteristic of the oöspore of most species of the genus. Lagerheim (1900) states that in *Monoblepharis macrandra* the zygote may occasionally move away from the oögonium and exhibit amoeboid changes of shape. Rarely the flagellum of the male persists for a short time, but always for a briefer period than in *Monoblepharella*. This behavior has also been noted by Barnes and Melville (1932) although they do not believe as did Lagerheim that fertilization may occur outside the oögonium. Woronin (1904) found the oöspore to be composed of two main layers, exospore and endospore. The exospore, in turn, had two parts. Of these the inner, in *M. sphaerica*, was thick and colorless and was raised to form the bullations; the outer part was thin, brown, and did not cover the warts. In *M. macrandra*, however, the outer, brown layer covered the bullations. Within the exospore the living protoplasm was surrounded by a thin, nearly colorless, elastic wall (endospore).

As Lagerheim and, later, Laibach (1927) observed, the male and female nuclei in the egg do not fuse at once, but remain side by side (Fig. 36 L-O, p. 450) until wall formation has reached an advanced stage and the bullations are beginning to take shape. Fusion then occurs, and the mature oöspore is uninucleate (Fig. 36 P-Q).

Only a few instances of germination of the oöspore have been observed. In several oöspores which were estimated to be not more than a month old (Sparrow, 1933b) the wall of the spore had cracked open and a single hyphal tube had been produced. Under the existing conditions only mycelium was formed (Fig. 39 H, p. 466). No

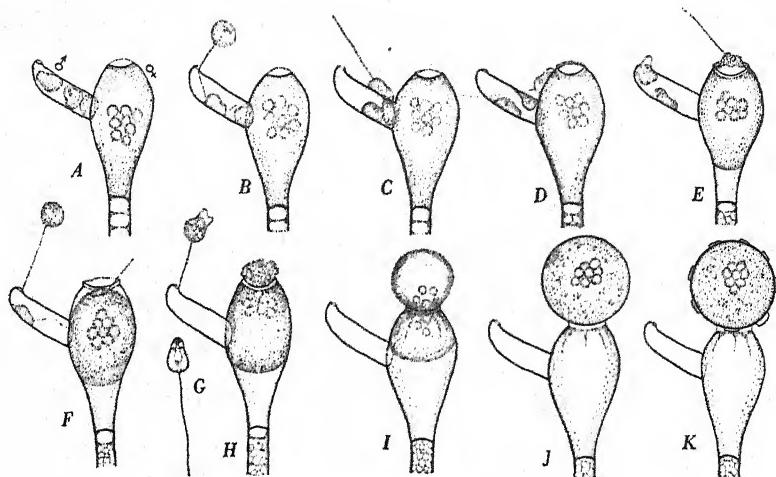


FIG. 37. Sexual reproduction in *Monoblepharis polymorpha* Cornu

A-B. Emergence of antherozoid from antheridium. *C-D.* Antherozoid creeping toward receptive spot of oögonium; oögonial wall around receptive papilla has begun to dilate. *E-F.* Antherozoid being engulfed by oöplasm, after which oöplasm retreats into oögonium. *G.* Antherozoid in motion; note difference in internal structure from that of amoeboid antherozoid. *H-J.* Emergence of fertilized egg from oögonium; protoplasm of antherozoid may still be distinguished. *K.* Early stage in formation of bullate wall of oöspore. (All $\times 670$.)

(Sparrow, 1933b)

other type of germination was seen either by Lagerheim or Laibach. According to the latter, in *Monoblepharis macrandra* the large resting nucleus of the oöspore (Fig. 36 Q, p. 450) may divide into as many as sixteen perceptibly smaller nuclei. No mitotic figures were apparent, but it was supposed that reduction took place during the first division (Fig. 36 R). Upon the formation of the germ tube the nuclei migrate into it, and the vegetative mycelium is established (Fig. 36 S). Further cytological work is greatly needed on this and other critical points in the life cycle, particularly of an epigynous species.

Occasionally one finds, particularly in *Monoblepharis sphaerica*, smooth-walled endogenous resting structures (Fig. 39 C, p. 466). Whether or not these are unfertilized eggs which have developed

parthenogenetically, as has been suggested, awaits further investigation. Lagerheim has described the formation of "gemmae," consisting of somewhat rounded chains of hyphal segments, in *M. polymorpha*.

In *Monoblepharella*, oögonia and antheridia are frequently formed on somewhat shorter branches of the thallus than are the zoosporangia. The clavate or obpyriform oögonium may, like the sporangium, be at first terminal, but after sympodial branching of the hypha it may appear lateral. Both oögonium and antheridium develop in the same manner as do those of *Monoblepharis sphaerica*, that is, the rudiment of the terminal oögonium is formed first. After this is delimited another, more proximal, segment is separated from the supporting hypha by a cross wall. In most instances this basal segment has, before its delimitation, formed beneath the oögonium a short branch, which continues to increase in size as maturation proceeds. The mature oögonium is thin-walled and apparently without a prominent receptive papilla, although further observations are needed on this point. The contents of the large broadly ellipsoidal egg are highly characteristic and conspicuous by reason of the numerous prominent colorless refractive globules imbedded in the clear cytoplasm (Fig. 38 A-B, p. 456). Although usually only a single egg is formed in the oögonium, from two to six have occasionally been found. The mature antheridium, which may be produced singly or in basipetal series beneath the oögonium, consists of a cylindrical portion and a large lateral beaklike outgrowth formed from the previously mentioned branch. About from two to five strongly amoeboid posteriorly uniflagellated antherozoids are produced and escape through a pore at the tip of the beak. These may creep about after discharge or, like the zoospores, which they resemble in all but size, swim about in the medium. The early stages in the process of fertilization are like those of *Monoblepharis*. The antherozoid after reaching the apex of the fully mature oögonium becomes strongly amoeboid. Its contents assume a watery consistency and spread over the oögonial apex (Fig. 38 C). Numerous small vacuoles appear and disappear so rapidly as to give an appearance of cytoplasmic "boiling." The flagellum waves feebly above the body of the sperm and, as the cytoplasm of the male gamete gradually sinks into the oöplasm (Fig. 38 D-E), becomes more hyaline in appearance. During absorption of the male gamete the oöplasm expands and for a

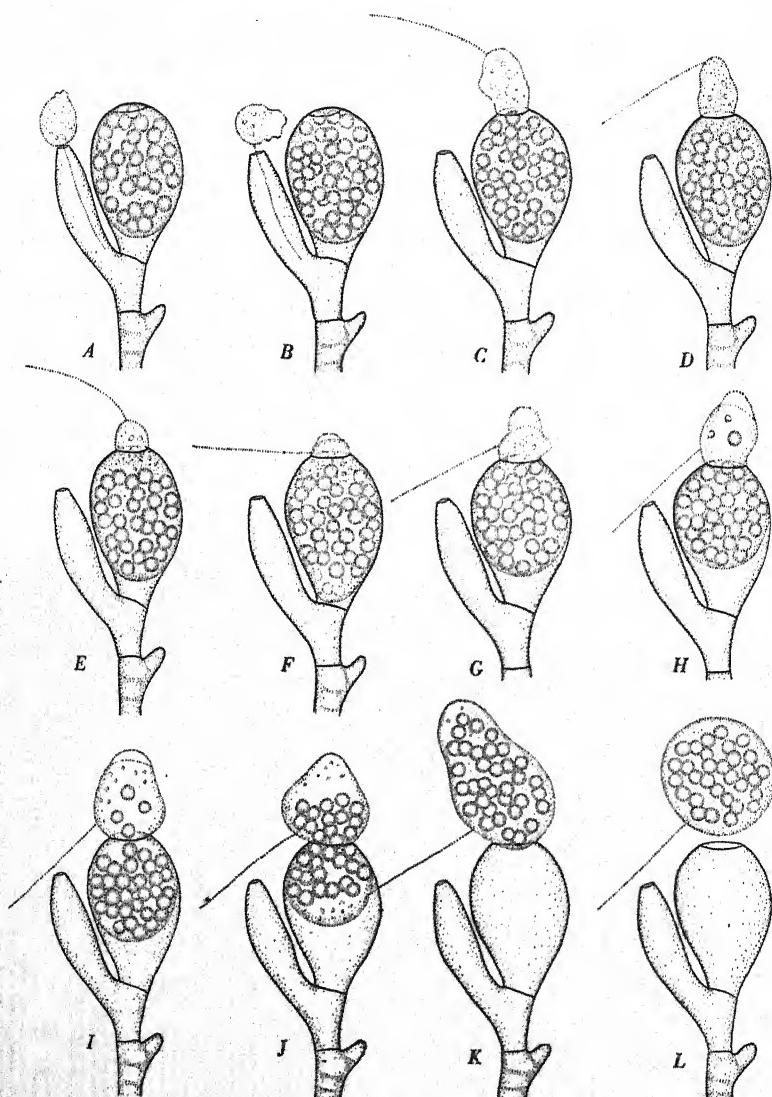


FIG. 38. Sexual reproduction in *Monoblepharella Taylori* Sparrow

A-B. Mature oogonium and last of four antherozoids emerging from hypogynous antheridium. C. Antherozoid making contact with egg. D-E. Stages in absorption of male gamete by egg. F. Zygote immediately before

short time fills the oögonium (Fig. 38 F). In none of the many instances of fertilization observed was the body of the male gamete completely absorbed by the oöplasm. There was always a small papilla-like part which persisted at the apex and from which protruded the flagellum of the antherozoid (Fig. 38 F). The remainder of the male gamete could be detected for a time as a slightly more granular material in the anterior part of the egg, but it was soon lost to view. Almost instantly after the absorption of the major part of the antherozoid the papilla-like residue of this structure on the surface of the egg started to increase in size (Fig. 38 G). This marked the initiation of evacuation of the zygote from the oögonium. More definite evidence of emergence could then be seen in the migration of the conspicuous globules into the enlarging papilla (Fig. 38 H-J). These continued to flow out with the cytoplasm of the zygote. Meanwhile, the flagellum remained passive, but slowly assumed a lateral position with respect to the orifice of the oögonium as the zygote oozed out. The completely emerged zygote was at first rather pyriform, with the flagellum nearly basal and extending at a right angle or more to the long axis of the body (Fig. 38 K). The zygote rounded off, remained quiescent for a few seconds, and then began to rock gently (Fig. 38 L). A trembling movement of increasing intensity was soon initiated, which frequently carried the zygote somewhat away from the oögonial orifice. Lateral vibration of the hitherto quiescent flagellum followed, and vacuoles appeared in the anterior part of the now more ovoid body. After a few violent tugs, accompanied by rapid vibration of the dark-appearing flagellum, the zygote began to rotate on its long axis as well as to progress forward; finally it swam slowly off. Under poor environmental conditions the zygote may fail to emerge, and the oöspore is formed in the oögonium.

After a period of motility of unknown duration, frequently punctuated by intervals of quiescence and strong amoeboid crawling, the zygote comes to rest. Its flagellum is apparently absorbed

emergence; a small part of body of male gamete and its flagellum persist, the flagellum having assumed a lateral position. *G.* Beginning of emergence of zygote. *H-K.* Further stages in emergence of zygote. *L.* Zygote rounding off and about to swim away from oögonium. (All approx. $\times 1000$.)

(Sparrow, 1940b)

and it is surrounded by a thickened wall. The globules persist for a time, but eventually these are assimilated and the oöspore undergoes a period of dormancy, far removed from the oögonium. The precise duration of encystment is not known. Fully mature oöspores dried for three months on cover slips have germinated when placed in water. It is probable, therefore, that the oöspore can remain viable in the soil during ordinary periods of tropical drought.

Upon germination a single small pore is formed in the oöspore wall, through which a hypha emerges. The hypha elongates indefinitely, branches, makes contact with bits of organic material, and reëstablishes the fungus. Reproductive organs of either type develop, or the mycelium may continue its vegetative growth.

No confirmation of the sexual process described by Cornu (1877b) as occurring in *Gonapodya prolifera*, has as yet been published, and the nature of the sexual stage of the genus, if it exists, is still in doubt. Further details are included under the discussion of *G. prolifera*.

SYSTEMATIC ACCOUNT

MONOLEPHARIDALES

MICROSCOPIC eucarpic fungi with a well-developed filamentous mycelium, the contents disposed in a reticulate or foamy manner, nonseptate save when reproductive organs are formed, or possessing pseudosepta; nonsexual reproduction by means of posteriorly uniflagellate zoospores borne in sporangia; zoospores usually with an anterior group of refractive granules; sexual reproduction, where known, oögamous, by means of posteriorly uniflagellate antherozoids borne in antheridia and nonflagellate oöospheres a single one of which is usually borne in each oögonium; the fertilized oösphere becoming a thick-walled oöspore, upon germination forming a hypha.

As originally conceived by Cornu, *Monolepharis* (including *Gonapodya*) embraced *Saprolegnia*-like organisms which had uniflagellate zoospores. Indeed, with the advent of more accurate observations on the zoospores of various filamentous Phycomycetes, there can be little question that this idea was a correct one. The

only other group of mycelial fungi with similar zoospores, the Blastocladiales, are unquestionably closely related to the Monolepharidales. This relationship is strikingly illustrated in *Allomyces* and *Blastocladia*, where the vacuolization of the hyphal cytoplasm and the development of the gametangia may at times be exactly like those of certain species of *Monolepharis*.

MONOLEPHARIDACEAE

Characters those of the order.

Members of *Monolepharis* and *Gonapodya* are found to be quite variable in nature, and it is frequently a difficult and puzzling matter to separate the species. For example, even in *M. sphaerica*, the best-defined species of *Monolepharis*, forms are occasionally found which are very like those of *M. polymorpha* and the closely related *M. macrandra*. In the genus *Gonapodya* variations and intergradations between the two known species may be so extensive as to make specific determination impossible.

Wide divergences in size are also frequent, and often a single plant will bear organs approaching or reaching the recorded limits for the species. Variations in this respect are, therefore, not considered particularly significant.

KEY TO THE GENERA OF THE MONOLEPHARIDACEAE¹

Hyphae without pseudosepta or constrictions; sexual reproduction

present or absent

Sexual reproduction present

Oöspores formed outside at the orifice of the oögonium or
within the oögonium; zygote not flagellate

MONOLEPHARIS, p. 460

Oöspores formed remote from the oögonium; zygote free-
swimming MONOLEPHARELLA, p. 470

Sexual reproduction not known MONOLEPHARIS, p. 460

Hyphae bearing pseudosepta which are generally constricted; sex-
ual reproduction apparently lacking GONAPODYA, p. 472

¹ This key presupposes that material has been subjected to conditions favorable for sexual and nonsexual reproduction. For *Myriolepharis* see pp. 475-476.

MONOBLEPHARIS CORNU

Bull. Soc. Bot. France, 18:59. 1871

(Figures 39-40, pp. 466, 468)

Diblepharis Lagerheim, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25,
Afd. 3, No. 8:39. 1900.*Monoblephariopsis* Laibach, Jahrb. wiss. Bot., 66:603. 1927.

Mycelium nonseptate, branched or unbranched, colorless or with a slightly brownish tinge, attached by rhizoids to the substratum, contents of the hyphae disposed in a reticulate or foamy manner; zoosporangia usually terminal, narrowly cylindrical or somewhat irregular in shape, cut off from the hyphae by cross walls, renewed by branching of the hyphae or by internal proliferation; zoospores fully formed within the sporangium, escaping after the dissolution of its apex, posteriorly uniflagellate; oögonia intercalary or terminal, usually narrowly pyriform to spherical, cut off from the attendant hyphae by cross walls, each oögonium exhibiting upon maturity a well-defined receptive papilla and a single egg; antheridia of differing shapes, usually somewhat cylindrical, variously placed, forming a small number of uniflagellate sperm entirely similar, save for their smaller size, to the zoospores; oöspheres after fertilization remaining in the oögonia or emerging, in either case developing into thick-walled oöspores; oöspore upon germination producing a new thallus.

Saprophytic primarily on vegetable debris, particularly twigs, also on animal remains.

The genus *Diblepharis* was established by Lagerheim to include *Monoblepharis fasciculata* and *M. insignis* Thaxter, which were described as having biflagellate zoospores. See, however, the remarks under the descriptions of these species (pp. 467, 469).

Monoblephariopsis was erected to include *Monoblepharis regignens* and *M. ovigera*, sporangial forms differing from other species in having more slender hyphae and smaller sporangia which proliferated, and in lacking sex organs. As these differences appear worthy only of specific distinction from the sporangial stages of other species of the genus (which occasionally proliferate), and as no sexual stage has as yet been found with certainty in this species, it seems better to replace them in *Monoblepharis* until further information on their life cycle is forthcoming.

KEY TO THE SPECIES OF MONOLEPHARIS

Sexual reproduction known, sex organs generally formed in abundance

Oöspores mostly exogenous, i.e. extruded from the oögonium and remaining attached at the orifice; rarely endogenous, i.e. remaining within the oögonium; antheridia variously borne

Antheridia usually hypogynous, i.e. formed immediately below the oögonium, or on separate branches

Antheridia scarcely exserted, nearly always accompanying the oögonia *M. sphaerica*, p. 461

Antheridia conspicuously exserted, in young plants occurring on separate branches from the oögonia, in older ones formed in groups with the oögonia

M. macrandra, p. 462

Antheridia epigynous, i.e. appearing to be inserted on the oögonia *M. polymorpha*, p. 464

Oöspores always endogenous, i.e. retained within the oögonium; antheridia epigynous

Sex organs in fascicles, plant not unusually large

M. fasciculata, p. 467

Sex organs linearly arranged, basipetal, plant very large

M. insignis, p. 467

Sexual reproduction unknown

Sporangia narrowly cylindrical, frequently proliferating

M. regnicens, p. 469

Sporangia more ovate, rarely proliferating *M. ovigera*, p. 470

MONOLEPHARIS SPHAERICA Cornu

Bull. Soc. Bot. France, 18:59. 1871; Ann. Sci. Nat. Bot., V, 15:82, pl. 2, figs. 1-6. 1872. Emend. Woronin, Mém. Acad. Impér. Sci. St. Peters., Phys.-Math. Cl., VIII, 16:1-24, pl. 1, figs. 1-16, pl. 2, figs. 17-19, 21-27, pl. 3, figs. 50-53. 1904

(Figure 39 C, p. 466)

Mycelium well developed, consisting of cylindrical, somewhat rigid, usually sparingly branched hyphae 7.5μ in diameter in the stouter basal portions, tapering distally to 2μ ; sporangia narrowly cylindrical, $72-104 \mu$ in length by $5.4-7.2 \mu$ in diameter, borne singly in a terminal position or in groups; zoospores $5.4-9 \mu$ in length by $3.2-5.4 \mu$ in diameter; oögonia narrowly pyriform to subspherical,

occurring singly, terminally, or in a linear series alternating with the antheridia, 18–45 μ in length by 8–19 μ tapering to 5.4–16 μ in diameter; antheridia narrowly cylindrical, hypogynous, opening by a slightly exserted tube formed just beneath the oögonial cross wall, 9–18 μ in length by 3.6–9 μ in diameter, antherozoids from four to seven, about 3.6 μ in length by 1.5–2 μ in diameter; oöspores usually exogenous, thick-walled, brown, 12.6–27 μ in diameter, covered by light-yellow bullations 1.5–2 μ in height, germination not observed.

On submerged twigs of various types, leaves of conifers, animal material. *Cornu* (*loc. cit.*), FRANCE; *Woronin* (*loc. cit.*), FINLAND; Laibach (1927 : fig. 8), Höhnk (1935), GERMANY; Thaxter (F.), Sparrow (S.) (1932b:290, pl. 7, fig. F; 1933b:528, pl. 20, figs. 1–4, 29; 1933c:530), (coll. Linder) Sparrow (1933b), UNITED STATES; Apinis (1930:237), LATVIA; Barnes and Melville (1932:84, fig. 1), Sparrow (1933b:529; 1936a:459), ENGLAND.

Light-brown smooth-walled endogenous resting bodies about 28 μ long by 15 μ in diameter are occasionally found.

The oöspores of *Cornu*'s fungus, with one exception, were all endogenous. As was pointed out by *Woronin*, under favorable environmental conditions the oöspores are exogenous. All gradations between endogenous and exogenous may be found in a single pustule of the fungus, and occasionally on a single plant.

MONOLEPHARIS MACRANDRA (Lagerheim) Woronin

Mém. Acad. Impér. Sci. St. Peters., Phys.-Math. Cl., VIII, 16:13, pl. 2, figs. 32–46, pl. 3, figs. 47–49, 54–70. 1904

(Figure 39 E, p. 466)

Monoblepharis polymorpha Cornu, pro parte, Ann. Sci. Nat. Bot., V, 15:84, pl. 2, figs. 10–32. 1872; van Tieghem, Traité de Botanique (1874 ed.), figs. 167 C, 7 p–q. Paris.

Monoblepharis polymorpha var. *macrandra* Lagerheim, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:35, pl. 1, figs. 2, 4, 21–24, 36–46, 48–51, 54, 63, 67–68, pl. 2, figs. 11–26. 1900.

Mycelium filamentous, exceedingly well developed, consisting of rather flexuous nearly isodiametric profusely branched hyphae which under excellent conditions for growth may interlock and completely envelop the substratum, hyphae 5 μ tapering distally to 1.5–2 μ in

diameter, bearing occasional irregular swellings; sporangia narrowly cylindrical, 45–130 μ in length by 4.5–6 μ in diameter, occurring singly at the tips of the hyphae or grouped in sympodial or fasciculate fashion, occasionally proliferating; zoospores 7.8 μ in diameter by 9–12 μ in length; oögonia broadly cylindrical to narrowly pyriform, at first formed singly in a terminal or intercalary position, later occurring sympodially or more commonly in fascicles associated with antheridia; antheridia cylindrical, at first formed at the tips of hyphal branches other than those bearing oögonia, later occurring with them, always strongly exserted, variable in size, usually about 25–35 μ long by 5–7 μ in diameter; antherozoids from five to fourteen in an antheridium, about 6 μ in length by 4 μ in diameter; oöspores normally exogenous, having a tendency to fall away from the oögonium, 13–25 μ in diameter, the brown wall covered by lighter-colored bullations 1.5–2 μ in height, germination not observed.

Saprophytic on submerged twigs of various types. Lagerheim (*loc. cit.*), SWEDEN; Woronin (*loc. cit.*), FINLAND; Cornu (*loc. cit.*), FRANCE; Tiesenhausen (1912:266), SWITZERLAND; Petersen (1909: 399; 1910:535, fig. 15c), Lund (1934:45), DENMARK; Minden (1915: 476), Laibach (1926: figs. 1–3; 1927: text figs. 5, 7b, 9–10, pl. 12, figs. 1–19, 28–35, pl. 13, figs. 36–47), Höhnk (1935:219), GERMANY; Wettstein (1921), AUSTRIA; Thaxter (F.), Sparrow (S.) (1933b:530, text fig. 1 s-u, pl. 20, figs. 5–6, 25, 31; 1933c:530), UNITED STATES; Scherffel (1931:137), HUNGARY; Barnes and Melville (1932:86, text figs. 2–5), Sparrow (1933b:530; 1936a:459), ENGLAND.

If one combines the description of variations found in *Monoblepharis polymorpha* given at the top of page 84 of Cornu's monograph with the figures shown by him in this paper and in van Tieghem's *Traité de Botanique*, there seems little question that he observed this species. Lagerheim considered it to be a variety of *M. polymorpha*, but because of the position of the antheridium, its strong exsertion, and the tendency of one or the other of the sex organs to be formed in groups little chance exists of confusing this species with others of the genus. Forms are occasionally found, however, which produce antheridia approximating those of the closely related *M. sphaerica*, and, rarely, epigynous ones are observed. The determination of whether or not these variations are due to hybridism, as has been suggested, awaits further study.

MONOBLEPHARIS MACRANDRA var. *LAEVIS* Sparrow, Ann. Bot. London, 47:531, pl. 20, figs. 14-16. 1933. (Figure 39 G, p. 466.)

Thallus and reproductive organs like those of *Monoblepharis macrandra*; oöspore spherical, 25μ in diameter, dark brown, smooth-walled, contents bearing numerous globules.

On rose fruits, Sparrow (*loc. cit.*), UNITED STATES; twigs of *Aesculus*, Sparrow (*loc. cit.*), ENGLAND; *Fraxinus*, Sparrow (1936a:459), DENMARK.

MONOBLEPHARIS POLYMORPHA Cornu

Bull. Soc. Bot. France, 18:59. 1871; Ann. Sci. Nat. Bot., V, 15:83, pl. 2, figs. 7-9. 1872; van Tieghem, Traité de Botanique (1874 ed.), fig. 167 B, 4 (sporangia), and fig. 167 C, 7 l-n, and 9. Paris (Figure 39 A-B, p. 466)

Monoblepharis brachyandra Lagerheim, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:37, pl. 1, figs. 1, 3, 5-10, 14-20, 35-45, 47, 52-53, 55-62, 64-66, pl. 2, figs. 6-10. 1900.

Monoblepharis brachyandra var. *longicollis* Lagerheim, *loc. cit.*, p. 38, pl. 1, fig. 53, pl. 2, figs. 1-5. 1900.

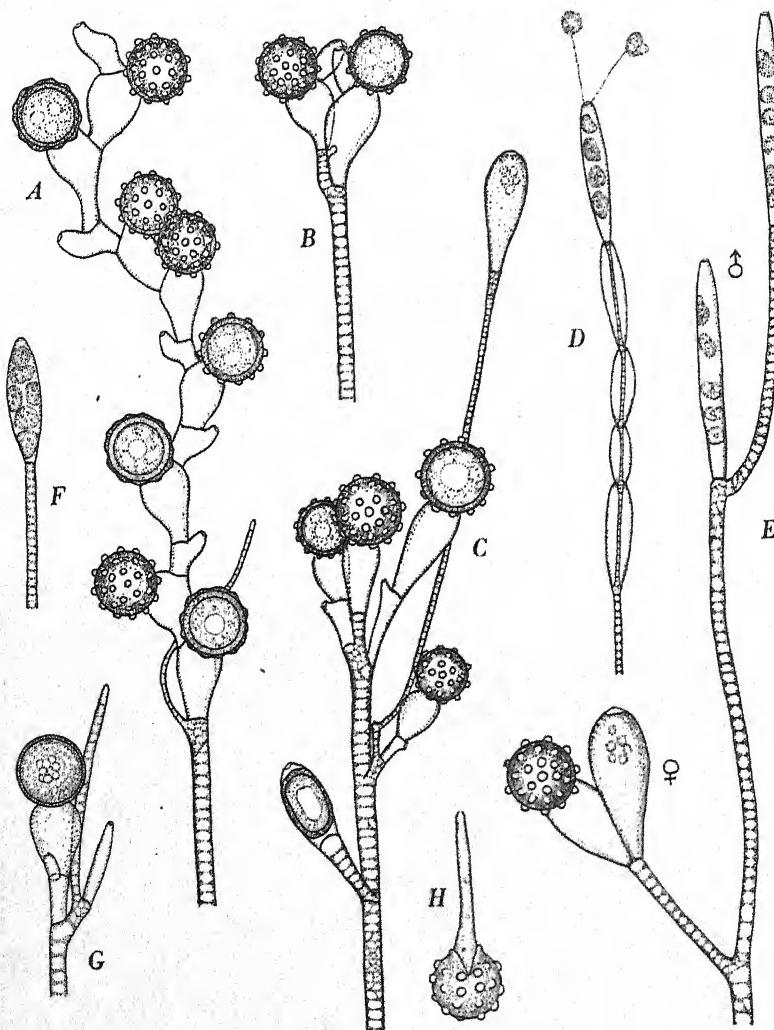
Mycelium filamentous, well developed, consisting of somewhat rigid cylindrical rather frequently branched hyphae which, in their stouter, basal portions attain a diameter of $12-15 \mu$, tapering distally to $1.5-2 \mu$; sporangia narrowly cylindrical, rarely somewhat irregular, $130-234 \mu$ in length by $10.4-13 \mu$ in diameter, occurring singly, terminally, or occasionally in clusters sympodially arranged; zoospores $10.4-13 \mu$ in length by $7.8-10.4 \mu$ in diameter; oögonia in young material broadly to narrowly pyriform, in older plants differing somewhat in shape, the even contour often being notched at the point of insertion of the antheridium, variable in size, usually $20-28 \mu$ long by $20-28 \mu$ tapering proximally to $5-7 \mu$ in diameter; antheridia epigynous but often in a series of incompletely developed sex organs appearing hypogynous, when terminal, somewhat cylindrical, when intercalary, somewhat geniculate with a broadly conical apex, varying greatly in size, usually about $10-35 \mu$ in length by $5-10 \mu$ in diameter; antherozoids from five to seven, each about 5.2μ in length by 2.6μ in diameter; oöspores spherical, nearly always exogenous, with a thick brown wall beset with bullations $1.5-2 \mu$ in height, or oftentimes with

light-colored undulations, 12–25 μ in diameter; oöspore germinating by means of a hypha.

Saprophytic on submerged twigs of various types and on animal remains. *Cornu* (*loc. cit.*), FRANCE; *Lagerheim* (*loc. cit.*), SWEDEN; *Woronin* (1904), FINLAND; *Tiesenhausen* (1912:265, fig. 1), SWITZERLAND; *Petersen* (1909:400; 1910:535, fig. 15 a–b), *Lund* (1934:46, fig. 22d), *Sparrow*, DENMARK; *Claussen* (1912), *Minden* (1902:806), *Laibach* (1927:601, fig. 2), GERMANY; *Apinis* (1930:237), LATVIA; *Wettstein* (1921), AUSTRIA; *Thaxter* (F.), *Sparrow* (S.) (1933b:529, text fig. 1 a–m, r, text fig. 2 a–k, pl. 20, figs. 7–13, 19–20, 28 [this species?], 36, 38–39; 1933c:530), UNITED STATES; *Barnes* and *Melville* (1932: fig. III, 3), ENGLAND.

Monoblepharis brachyandra is said to be distinct from *M. polymorpha* chiefly in the uneven contour of the oögonium at the place of insertion of the shorter stouter antheridium and in the frequently intercalary position of the latter, or, when epigynous, its tendency to be formed on the lower third of the oögonium. The oöspores differ in being smaller and in having flatter broader bullations, which may, in some specimens, be only slight undulations. Such differences are readily apparent when one has only a limited amount of material, in early stages of development. If large amounts of the fungus are available, however, and if the plants are observed over a long period of time, these differences become less distinct. One finds that whereas in the sex organs first formed the antheridia and oögonia are often disposed in a definite manner and possess definite, uniform shapes, in subsequent "generations" of such organs on the same hypha these characters vary considerably. Indeed, one may find combinations of *polymorpha* and *brachyandra* characters on a single plant. Such combinations are evident in *Lagerheim*'s figures of his species. These remarks apply also to the variety *longicollis*, which is based chiefly on slight differences in size, shape, and position of the sex organs and stronger bullations on the somewhat smaller oöspore. Variations are so prevalent in plants with a profuse development of sex organs that nearly every group of the latter might be considered a variety if based on such slight differences. Gemmae have been described by *Lagerheim* as occurring in *M. polymorpha*.

As originally described by *Cornu* *Monoblepharis polymorpha* was sufficiently inclusive to embrace *M. macrandra*.

FIG. 39. *Monoblepharis*

A-B. *Monoblepharis polymorpha* Cornu. C. *Monoblepharis sphaerica* Cornu. D. Proliferating zoosporangia of *Monoblepharis regnens* Lagerheim. E. Antheridia and oögonia of *Monoblepharis macrandra* (Lagerheim) Woronin. F. Mature sporangium of *Monoblepharis ovigera* Lagerheim. G. *Monoblepharis macrandra* var. *laevis* Sparrow. H. Germinating oöspore of *Monoblepharis polymorpha* Cornu. (All $\times 375$.)

(Sparrow, 1933b)

MONOLEPHARIS FASCICULATA Thaxter

Bot. Gaz., 20:439, pl. 29, figs. 8-12. 1895

(Figure 40 E, p. 468)

Diblepharis fasciculata (Thaxter) Lagerheim, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:40. 1900.

Hyphae straight, rigid, cylindrical, simple or, rarely, branched at the tips, 1-2 mm. long by 6 μ in diameter; antheridia narrow, tapering slightly, straight not divergent; antherozoids about sixteen in an antheridium, 3 μ in diameter; oögonia evenly oval-oblong or elliptical, the neck small and prominent, usually shorter than the antheridia, which are always present and single and terminal or borne superimposed on short crowded branches from the tips of the fertile hyphae; oöspores more or less regularly oval-oblong or elliptical, smooth, pale amber-brown, maturing within the oögonium, 22 \times 18 μ ; zoosporangia like the oögonia, bearing antheridia, the zoospores biflagellate (?), about 5-6 μ in diameter. (Modified from Thaxter.)

On submerged sticks with *Monoblepharis insignis*. Thaxter (F.) (*loc. cit.*), UNITED STATES; Thomas (1939:124, fig. 1), WALES.

This species is "distinguished from the last [*Monoblepharis insignis*] by its constantly smaller size and the greater regularity and different form of its sexual organs, as well as by its fasciculate habit" (Thaxter, *loc. cit.*).

The flagellation of the zoospores in this species as well as in *Monoblepharis insignis* should be further investigated. The biflagellate bodies borne in organs similar to oögonia are very different from zoospores in shape and much too small in comparison with the sperm to be consistent with what is found in other species of the genus. It is possible that they are extraneous, parasitic, organisms.

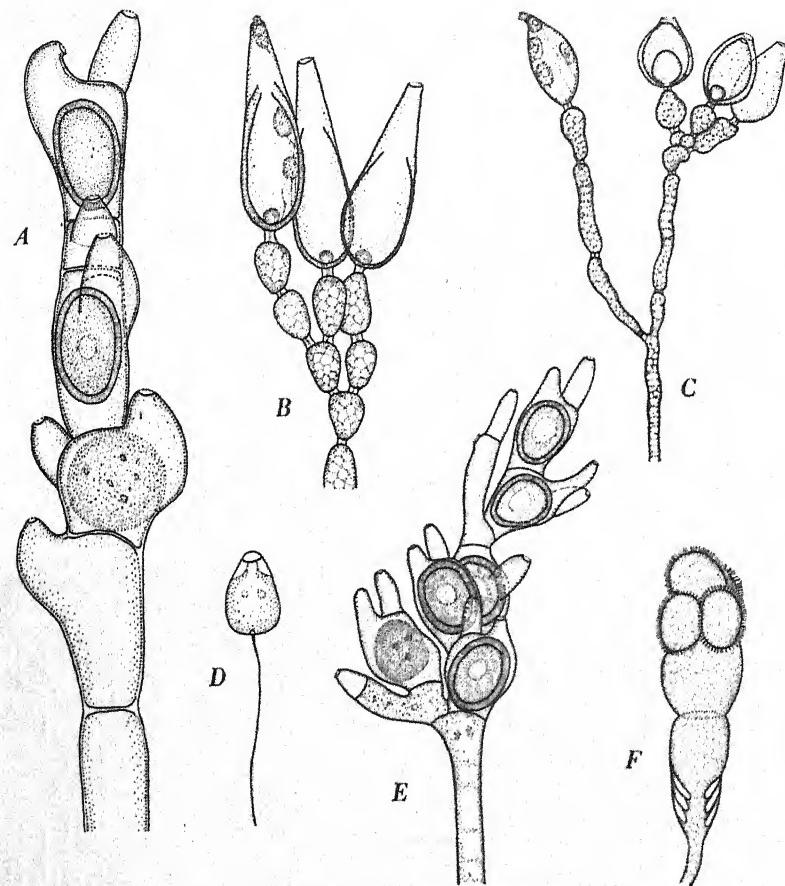
MONOLEPHARIS INSIGNIS Thaxter

Bot. Gaz., 20:438, pl. 29, figs. 1-7. 1895

(Figure 40 A, p. 468)

Diblepharis insignis (Thaxter) Lagerheim, Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:40. 1900.

Hyphae straight, rigid, hyaline or very pale reddish brown, nearly cylindrical, 1.5-2.5 mm. in length by 8-15 μ in diameter, rarely branched; antheridia broad, subconical to subcylindrical, straight or

FIG. 40. *Monoblepharidaceae*

A. Monoblepharis insignis Thaxter ($\times 375$), tip of hypha bearing epigenous antheridia and beaked oögonia, within which are endogenous oöspores (type material). *B. Gonapodya prolifera* (Cornu) Fischer ($\times 280$), part of plant, showing hyphal segments and proliferated zoosporangia. *C. Gonapodya polymorpha* Thaxter ($\times 280$), part of plant, showing a discharging sporangium and proliferated ones. *D. Zoospore of Gonapodya prolifera* (Cornu) Fischer ($\times 675$). *E. Monoblepharis fasciculata* Thaxter ($\times 375$), tip of hypha showing arrangement of sex organs, and endogenous oöspores (type material). *F. Myrioblepharis paradoxa* Thaxter, tip of hypha bearing zoosporangia, with multiflagellate zoospores being discharged from uppermost sporangium.

(*A-E*, Sparrow, 1933b; *F*, Thaxter, 1895b)

slightly divergent, the rounded tip often bent slightly inward, nearly symmetrical or often with base irregularly protruded on its inner side; antherozoids numerous (from twenty-four to thirty-two, approximately), uniflagellate; oospores maturing within the oogonium, smooth, pale amber-brown, spherical to long-oblong or irregular in outline, $30-45 \times 22-33 \mu$; oogonia single or several superimposed at the tips of the hyphae, irregular in form; zoosporangia rare, similar to the oogonia, zoospores biflagellate (?), about $10-12 \mu$ in diameter. (Modified from Thaxter.)

On submerged sticks in pools and ditches. Thaxter (F.) (*loc. cit.*), UNITED STATES; Thomas (1939:124, figs. II-III), WALES.

The zoospores described and figured for this species were not, presumably, seen to emerge; hence the flagellation is doubtful.

This and *Monoblepharis fasciculata* are indeed remarkable members of the genus. In their relatively enormous size, slight brown coloration of the protoplasm, process of fertilization involving discharge of a substance from the oogonium apparently attractive to the sperm, and smooth endogenous oospores, they are strikingly different from other species of the genus.

MONOLEPHARIS REGIGNENS Lagerheim

Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:39, pl. 1, figs. 11-13.
1900

(Figure 39 D, p. 466)

Monoblephariopsis regignens (Lagerheim) Laibach, Jahrb. wiss. Bot., 66:603, text fig. 4, pl. 12, figs. 20-27. 1927.

Mycelium exceedingly tenuous, sparingly branched, hyphae about 5μ at the base, tapering to $1.8-2 \mu$ in diameter; sporangia narrowly cylindrical, but distinctly broader than the hyphae, on which they are usually terminally placed, $18-36 \mu$ in length by $5.4-7.2 \mu$ in diameter, new sporangia formed by proliferation partly or wholly through the apex of the old one or occasionally by cymose branching; zoospores 8μ long by 5μ in diameter; sexual reproduction not observed.

Saprophytic on submerged twigs of various types. Lagerheim (*loc. cit.*), SWEDEN; Thaxter (F.), Sparrow (1933b:534, pl. 20, fig. 26; 1933c:530), UNITED STATES; Laibach (*loc. cit.*), Höhnk (1935:220, fig. 1 a-b), GERMANY; Sparrow (1933b:534), ENGLAND.

This and the following species may belong in *Monoblepharella*. See the remarks under the generic description of *Monoblepharis*.

MONOBLEPHARIS OVIGERA Lagerheim

Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 25, Afd. 3, No. 8:39, pl. 1, figs. 69-70.

1900

(Figure 39 F, p. 466)

Monoblephariopsis ovigera (Lagerheim) Laibach, Jahrb. wiss. Bot., 66: 609. 1927.

Monoblephariopsis oblongata Höhnk, Abhandl. Naturwiss. Vereins Bremen, 29 (3):221, fig. 1 c-h. 1935.

Mycelium often profuse, composed of very delicate occasionally branched hyphae 3-4 μ in diameter; zoosporangia terminal or intercalary, ovoid, 10-13 μ in diameter by 23-33 μ in length, rarely proliferating; zoospores often formed in two rows, 8 μ long by 6 μ in diameter; sexual reproduction not observed.

Saprophytic on submerged twigs of various types. Lagerheim (*loc. cit.*), SWEDEN; Sparrow (1933b:535, pl. 20, figs. 23, 33, 35, 37; 1933c:530), UNITED STATES; Sparrow (1933b:535; 1936a:459), ENGLAND; Höhnk (1935:221, fig. 1 c-h), GERMANY.

Höhnk's species appears to differ in no essential features from *Monoblepharis ovigera*. Though proliferation of the sporangium in the latter is rare it is by no means lacking. It is possible that the very small structures resembling sexual organs and the smooth-walled spherical cysts found by Sparrow (1933b: pl. 20, figs. 21-22, 24, 27) among sporangial plants of this species indicate that it has a type of sexual reproduction similar to that of *Monoblepharella Taylori*.

EXCLUDED SPECIES OF MONOBLEPHARIS

* MONOBLEPHARIS LATERALIS Hine

Amer. Quart. Micro. Journ., 1:141, pl. 7, figs. 4-21. 1878-79

This is doubtless a saprolegniaceous fungus, probably infected by a flagellate, a situation also found in *Archilegnia* (see p. 514 n.).

MONOBLEPHARELLA SPARROW¹

Allan Hancock Pacific Expeditions, Publ. Univ. So. Calif., 3(6):103. 1940

(Figure 38, p. 456)

Mycelium, contents, zoosporangia, oögonia, antheridia, and antherozoids as in *Monoblepharis*; the egg after fertilization emerging

¹ See also *Monoblepharella mexicana* Shanor, *Mycologia*, 34:242. 1942.

from the oögonium and by means of the persistent flagellum of the male gamete undergoing a period of swarming, after which it encysts and becomes a thick-walled oöspore; the oöspore upon germination forming the vegetative mycelium.

Saprophytic in tropical soils.

Because of the remarkable behavior of the zygote in *Monoblepharella Taylori* the organism has been segregated from *Monoblepharis* and a new genus has been erected to accommodate it. It is possible that *Monoblepharis ovigera* and *Monoblepharis regignens* may in the future be found to possess this same type of sexual reproduction, when they too might be included in *Monoblepharella*.

MONOBLEPHARELLA TAYLORI Sparrow

Mycologia, 31:737. 1939; Allan Hancock Pacific Expeditions, Publ. Univ. So. Calif., 3(6):103, pls. 16-17. 1940

Mycelium well developed, consisting of tenuous flexuous branched hyphae 2-5 μ in diameter, the contents reticulately vacuolated; sporangia narrowly siliquiform, with a tenuous wall, variable in size, 35-65 μ long by 5-9 μ in diameter, with a very narrow (2.5-4 μ) base, occurring singly or in pairs at the tips of the hyphae or after sympodial branching of a hypha appearing lateral; zoospores ovoid or somewhat cylindrical, 7-9 μ long by 4.5-5 μ wide, the posterior flagellum from two to three times the length of the body; oögonium at first terminal or after sympodial branching of the supporting hypha often appearing lateral, clavate or obpyriform, with rounded apex and narrow cylindrical base, 15-17 μ long by 8-10 μ wide tapering to 2-3 μ at the base, the contents at maturity forming one or occasionally up to four eggs containing numerous large refractive globules; antheridia hypogynous, often several developed in basipetal succession, consisting of a cylindrical segment of the suboögonial hypha and a beaklike lateral outgrowth 8-10 μ long by 4-5 μ wide; antherozoids two to five, strongly amoeboid, posteriorly uniflagellate, ovoid when swimming and about 5 μ long by 3 μ wide, escaping through a pore formed at the tip of the beak; zygote broadly ovoid to nearly spherical, 10-13 μ long by 8-10 μ wide, posteriorly uniflagellate, free-swimming, the contents bearing numerous large refractive globules; oöspore formed free in the water, spherical, 8-11 μ in diameter, with a slightly thickened light-brown smooth wall, contents bearing globules, forming a mycelium upon germination.

In soil, coll. W. R. Taylor, BRITISH WEST INDIES, PANAMA; coll. C. D. La Rue, NICARAGUA.

The sporangial stage of this species strongly resembles that of *Monoblepharis ovigera*, which, so far as is known, lacks a sexual stage.

GONAPODYA FISCHER

Rabenhorst. Kryptogamen-Fl., 1(4):382. 1892

(Figure 40 B-D, p. 468)

Mycelium irregularly or dichotomously branched, varying in extent of development, frequently profuse, method of attachment to the substratum probably by rhizoids, composed of cylindrical, often moniliform hyphal segments delimited by hyaline constricted pseudosepta, hyphae with a reticulate or foamy, or sometimes homogeneous, disposition of the protoplasm; zoosporangia terminal, occurring singly or in fascicles, internally proliferous, varying in shape; zoospores completely formed within the sporangium, escaping upon the deliquescence of the apex of the latter, ovoid to cylindrical, posteriorly uniflagellate, possessing an internal organization similar to that of *Monoblepharis*; sexual reproduction (according to Cornu) by means of oögonia and antherozoids.

Saprophytic primarily on submerged twigs and fruits.

When the sexual stage of this genus is known in greater detail the species may more properly be placed in another order, perhaps the *Blastiocladiales*. In view, however, of the vacuolization of the protoplasm, the formation, discharge, and structure of the zoospores, and the account, by that excellent observer Cornu, of a sexual stage, it is probably best in this matter to follow Fischer, Schroeter, and Laibach, at least for the present.

KEY TO THE SPECIES OF GONAPODYA

- | | |
|----------------------------------|-------------------------------|
| Sporangia long-siliquiform | <i>G. prolifera</i> , p. 472 |
| Sporangia long-ovoid | <i>G. polymorpha</i> , p. 474 |

GONAPODYA PROLIFERA (Cornu) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):382. 1892

(Figure 40 B, p. 468)

Monoblepharis prolifera Cornu, Bull. Soc. Bot. France, 18:59. 1871; Ann. Sci. Nat. Bot., V, 15:16. 1872; in van Tieghem, Traité de Botanique (1874 ed.), fig. 167 B, 5. Paris.

Saprolegnia siliquaeformis Reinsch, Jahrb. wiss. Bot., 11:293, pl. 15, figs. 12-13. 1878.

Gonapodya siliquaeformis (Reinsch) Thaxter, Bot. Gaz., 20:480, pl. 31, figs. 6-10. 1895.

Mycelium composed of hyphae more or less regularly divided by pseudosepta into short-elliptical to long-clavate segments, copiously and successively subumbellately branched, the branches diverging in a dense tuft from a common base; sporangia once to many times proliferous, the secondary sporangia only slightly exserted, long, pod-shaped, inflated below, the sometimes very elongate distal portion tapering gradually to a blunt apex, borne sessile on the terminal cell of a branch or separated from it by a clearly defined constriction; zoospores variable in number, up to fifty or more in a sporangium, posteriorly uniflagellate, elliptical, or somewhat cylindrical; sexual reproduction (according to Cornu) by means of oögonia and antherozoids, oöspores oval in terminally perforate oögonia like the sporangia. (Modified from Thaxter.)

On decaying fruits and twigs of various types in water. Cornu (*loc. cit.*), FRANCE; Reinsch (*loc. cit.*), Minden (1915:577, fig. 12a; 1916: pl. 6, fig. 56), Laibach (1927:599, fig. 11), GERMANY; Thaxter (F.) (*loc. cit.*), Kanouse (1927:304), Sparrow (S.) (1932b:291, pl. 7 A; 1933b:535, pl. 20, figs. 30, 32; 1933c:530), apples, etc., Sparrow (MICHIGAN), UNITED STATES; Petersen (1909:397; 1910:533, fig. 11), Lund (1934:39), DENMARK; Valkanov (1931a:366), BULGARIA; Apinis (1930:236), LATVIA; Barnes and Melville (1932:93), Sparrow (1933b:535; 1936a:459, pl. 20, fig. 1), ENGLAND; Crooks (1937:220, fig. 7 b-d), AUSTRALIA.

This is a rather common and variable species, generally forming small white pustules on rosaceous fruits under very foul environmental conditions. Variations in the shape of the sporangium are extensive and may approach those typically observed in the following species (*Gonapodya polymorpha*).

Cornu (1877b) reported that in his fungus he found oval colorless oöspores borne in oögonia similar in shape to zoosporangia and produced from an oösphere fertilized by a sperm. No further information or figures were given. Thaxter has suggested that Cornu mistook unusually small zoospores for antherozoids, and that his oöspores were merely encysted, secondary sporangia. It is entirely possible that the two species of *Gonapodya* lack a sexual stage and that Cornu's "oöspore" was some sort of encysted sporangium. In

view of the small amount of investigation that this group has thus far been accorded, however, it seems quite useless to venture any opinion now concerning the matter.

GONAPODYA POLYMORPHA Thaxter

Bot. Gaz., 20:481, pl. 31, figs. 11-16. 1895

(Figure 40 C, p. 468)

Hyphae irregularly or more frequently dichotomously branched, more or less uniformly divided into short-oval or irregular segments, the segmented portion arising directly from the substratum or more often confined to tufts of branchlets borne subumbellately on the ends of slender elongate hyphae in which the segmentation is indistinct or obsolete, the segmentation frequently ill-defined or obsolete throughout the whole vegetative body; sporangia variable in size and form, long-oval, tapering rather abruptly to the blunt tip, terminal and solitary or sometimes several arising from a single segment, once to many times proliferous, the hyphae sometimes traversing and growing beyond the empty sporangium; zoospores somewhat variable in size and number, usually about 13μ long by 7μ in diameter; sexual stage unknown. (Modified from Thaxter.)

On submerged fruits of various types, especially those of the Rosaceae; submerged twigs of fir, spruce mucilage, and twigs of deciduous trees. Thaxter (F.) (*loc. cit.*), Sparrow (1932b:290, pl. 7, fig. L; 1933b:537, pl. 20, fig. 34; 1933c:530), Matthews (1935:309, pl. 63, figs. 1-3), UNITED STATES; Petersen (1909:398, figs. 12-14; 1910:534, figs. 12-14), Lund (1934:39), DENMARK; Apinis (1930:236), LATVIA; Minden (1915:578), GERMANY; Barnes and Melville (1932:93, fig. 6), Sparrow (1933b:537; 1936a:459, pl. 20, fig. 8), ENGLAND; Crooks (1937:221, fig. 7a), AUSTRALIA.

The general habit of this species is more open and ramoser than that of *Gonapodya prolifera*, and it is usually found under less foul environmental conditions than that species. Whether or not the difference in environment is responsible for the differences in the two fungi awaits further investigation.

Thaxter has described oöspores about 54μ in diameter with laminated refractive walls about 18μ thick as often occurring with *Gonapodya polymorpha*, although he was not successful in demon-

strating any definite connection between the two. These bodies have been considered by Minden (1916) to be the oospores of his *Pythiogeton utriforme*. Petersen (1910) has reported encysted zoospores, termed "resting spores," in the sporangia of *G. polymorpha*. As in the preceding species, it is probable that the sexual stage of this fungus has not yet been observed.

GENUS OF UNCERTAIN AFFINITIES, POSSIBLY ALLIED TO THE
MONOLEPHARIDALES

MYRIOBLEPHARIS THAXTER

Bot. Gaz., 20:482, pl. 31, figs. 1-5. 1895

(Figure 40 F, p. 468)

"Hyphae slender, sparingly branched, bearing terminally zoosporangia becoming many times proliferous and forming an elongate series traversed by the hypha from the successive proliferations of which they arise. Zoospores very large, multiciliate over their whole surface, resulting from the division of the contents of the sporangia which make their exit as a single ciliated mass surrounded by a gelatinous membrane attached to the distal end of the sporangium, the successive envelopes, after rupturing distally, persistent around the series of empty sporangia" (Thaxter, *loc. cit.*).

Saprophytic on submerged twigs.

Minden (1915:476), who states that he found this organism and cultivated it for a long time, remarks that it appears from his observations to be a mixture of a proliferous species of *Pythium* and a parasitic protozoan—presumably a flagellate. He points out that the mycelium when grown pure never forms in its sporangia large multiflagellate zoospores, but ones the size of *Pythium* zoospores.

MYRIOBLEPHARIS PARADOXA Thaxter

Bot. Gaz., 20:482, pl. 31, figs. 1-5. 1895

"Characters of the genus. The contents of the sporangium dividing into two or four (rarely more) zoospores which are carried upward by the discharged contents of the two sporangia subsequently formed before making their escape from their inclosing envelope. Hyphae

slender, flexuous, seldom more than once or twice branched, about 1 mm. long, $4-5 \mu$ in diameter, sometimes growing through the terminal sporangium of a series and subsequently producing a new series in a similar fashion. Zoospores broadly oval or oblong, $20-30 \mu \times 18-20 \mu$ " (Thaxter, *loc. cit.*).

On submerged sticks with *Monoblepharis*, etc., Thaxter (*loc. cit.*), UNITED STATES; Minden (1915:476), GERMANY.

FAMILY OF UNCERTAIN AFFINITIES

HYPHOCHYTRIACEAE

Microscopic aquatic fungi with a body plan resembling that of the Chytridiales, holocarpic or eucarpic, monocentric or polycentric, the vegetative system rhizoidal or hypha-like with intercalary swellings; zoospores anteriorly uniflagellate, for the most part maturing outside the sporangium; resting spores apparently asexually formed.

Confirmation of the anteriorly uniflagellate character of the zoospore in *Hypochytrium* by Valkanov (1929b) and Karling (1939b) and in *Rhizidiomyces* by Coker (1923) makes necessary the segregation of these fungi of obscure relationships from the true chytrids. On the hypothesis that the zoospore represents the most primitive condition, it is supposed that the members of the Hypochytriaceae have arisen from anteriorly uniflagellate monad ancestors and have undergone an apparently limited (so far as diversity of types is concerned) but nonetheless definitely parallel evolution with the posteriorly uniflagellate chytridiaceous series. This is strikingly demonstrated in *Latrostium*, whose sporangium and resting spore strongly resemble those of *Rhizophydium decipiens*, and also in the similarity in thallus structure of *Rhizidiomyces* and *Phlyctochytrium* and of *Hypochytrium* and the operculate chytrid *Megachytrium*.

Because of the small number of forms now known the erection of an order to include them does not seem necessary. It should be noted, however, that though *Latrostium* and *Rhizidiomyces* are alike in the character of their zoospores, they differ markedly in the manner of forming them, which indicates only a distant relationship. Further, both of these monocentric types are far removed from the strongly polycentric *Hypochytrium*. When more fungi belonging to this family are discovered their relations to one another and to the other Phycomycetes will be better understood.

The decision as to whether or not Fisch's *Olpidium Lemnae* belongs here awaits the results of further investigations on that organism to confirm the anterior position of the flagellum of the zoospore.

spore. The same applies to the terrestrial fungus, *Cystochytrium radicale* Cook (*Trans. Brit. Mycol. Soc.*, 16:251. 1932).

KEY TO THE GENERA OF THE HYPHOCYTRIACEAE

Thallus monocentric, eucarpic

Sporangium endobiotic, resting on the oöplasm of the egg of *Vaucheria*; zoospores formed in the sporangium; rhizoids appearing laterally attached..... LATROSTIUM, p. 478

Sporangium epibiotic; zoospores completing their maturation in a vesicle formed at the tip of the discharge tube; rhizoids arising from an endobiotic apophysis..... RHIZIDIOMYCES, p. 479

Thallus strongly polycentric, tubular..... HYPHOCHYTRIUM, p. 482

LATROSTIUM ZOPF

Beitr. Physiol. Morph. niederer Organismen, 4:62. 1894

(Figure 41 A-D, p. 481)

Thallus resting on and in the contracted oöplasm within the oögonium of the host, monocentric, eucarpic, consisting of the rudiment of the sporangium, which is sessile on the oöplasm, and a complex of extremely delicate much-branched rhizoids arising laterally at one place on the sporangial rudiment and penetrating the oöplasm; sporangium inoperculate, forming a broad discharge papilla; zoospores anteriorly uniflagellate, with a single globule, escaping fully formed through a broad apical pore which does not penetrate the host wall; resting spore borne like the sporangium, with a thick smooth radially striated exospore and a thin smooth endospore, contents with an extremely large globule, germination not observed.

Parasitic in oögonia of *Vaucheria*.

The genus is founded on a species so like *Rhizophyidium decipiens* in habitat, shape of the sporangium, method of discharge, and structure of the resting spore that it seems hardly probable that two organisms can be so alike in all characters except the flagellation of the zoospore. Since the observations on zoospore flagellation come from so high an authority as Zopf, however, we are forced to assume their correctness, at least until further investigations disprove them.

LATROSTIUM COMPRIMENS Zopf

Beitr. Physiol. Morph. niederer Organismen, 4:62, pl. 3, figs. 6-19. 1894

Sporangia from one to six in a host cell, broadly lenticular, with a delicate smooth colorless wall which collapses after discharge of the

zoospores and a broad apical papilla; rhizoids extremely delicate, much branched; zoospores irregularly ovoid, 2.5–3 μ in diameter, with a large colorless globule, the broader, anterior end bearing a long flagellum, escaping individually through a wide apical pore, movement evenly swimming, not hopping; resting spore broadly lenticular, 30–50 μ in diameter, outer wall thick, colorless, smooth, radially striated, giving a cellulose reaction, inner wall thin, homogeneous, contents with an extremely large globule that nearly fills the lumen, rhizoids delicate, much branched, germination not observed.

In oögonia of *Vaucheria sessilis*, *V. terrestris*, GERMANY.

De Wildeman (1895a:63) has described ovoid resting spores with striated walls found in oögonia of *Vaucheria sessilis* from Belgium and Switzerland as belonging to this species. Since the sporangia were not observed, however, it is equally possible that these organisms belong to *Rhizophydiump decipiens*. Scherffel (1926a:221) claims that the resting spores of the two species, which in all other respects are identical (no rhizoids, however, have been observed as yet in *R. decipiens*), may be distinguished by the fact that in *Latrostium* there is a giant globule in the contents, whereas in *R. decipiens* there are numerous small ones. The validity of this fine distinction can only be determined after both forms have been thoroughly investigated. Resting spores of both types have been found in the same oögonium in *Vaucheria terrestris* in Michigan.

RHIZIDIOMYCES ZOPF

Nova Acta Acad. Leop.-Carol., 47:188. 1884

(Figure 41 E–G, p. 481)

Thallus epi- and endobiotic, monocentric, eucarpic, the epibiotic part forming the rudiment of the sporangium, the endobiotic part the apophysis and branched rhizoidal system or the rhizoidal system alone; sporangium sessile, inoperculate, with a pronounced discharge tube; zoospores partly delimited within the sporangium, discharged into an evanescent vesicle formed at the orifice of the tube, final maturation completed in the vesicle, anteriorly uniflagellate, with a minute refractive granule; resting spore not observed.

On eggs and oöspores of aquatic Phycomycetes and on green algae, and saprophytic in soil.

The genus is of great interest because of the strikingly chytridaceous habit, which resembles that of *Phlyctochytrium*.

KEY TO THE SPECIES OF RHIZIDIOMYCES

Sporangium wall persistent after discharge; on eggs and oöspores of other aquatic Phycomycetes or saprophytic in soil

On eggs and oöspores of aquatic Phycomycetes; apophysis present

R. apophysatus, p. 480

In soil; apophysis absent; rhizoids usually arising from a main axis

R. bivellatus, p. 480

Sporangium wall evanescent after discharge; on *Chlamydomonas*

R. Ichneumon, p. 482

RHIZIDIOMYCES APOPHYSATUS Zopf

Nova Acta Acad. Leop.-Carol., 47:188, pl. 20, figs. 1-7. 1884

(Figure 41 E-G)

Sporangium spherical, subspherical, or broadly pyriform, 18-45 μ in diameter, wall stout, smooth or with short spines, colorless or faintly golden brown, with an apical or subapical long cylindrical discharge tube; rhizoids richly branched, arising from one or two stout main axes at the base of a pyriform, or occasionally spherical or fusiform, subsporangial apophysis up to 18.5 μ in diameter; zoospores ovoid or oblong with rounded ends, 3.7-6 μ (long?), with a few minute gleaming granules and a short anterior flagellum, movement swimming or feebly amoeboid; resting spore not observed.

Parasitic on oögonia of *Saprolegnia ferax*, *S. asterophora*, *Achlya polyandra*, Zopf (*loc. cit.*), GERMANY; *Achlya conspicua*, *A. apiculata*, Coker (1923:186, pl. 63), "Saprolegnian," cultivated on pollen of *Liquidambar*, nutrient agar, Couch (1939a), *Achlya* sp., Sparrow (1932b:282, fig. 3e), UNITED STATES; *Achlya flagellata*, Tokunaga (1934b:391, pl. 11, fig. 10), JAPAN; host (?), Forbes (1935b:3), ENGLAND; *Achlya Klebsiana*, Chaudhuri and Kochhar (1935:150, pl. 12, figs. 24-29), INDIA.

RHIZIDIOMYCES BIVELLATUS Nabel

Arch. f. Mikrobiol., 10:537, figs. 1-7. 1939

Sporangium spherical, 80-100 μ in diameter, wall smooth, in young plants of two layers the inner wall of chitin and evanescent, the outer of cellulose and persistent, discharge tube apical, up to 300 μ long by 10 μ in diameter; rhizoids richly branched, arising from one or more axes at the base of the sporangium; apophysis apparently lacking; zoospores oblong-ellipsoidal, 8 μ long by 6 μ broad, with a single

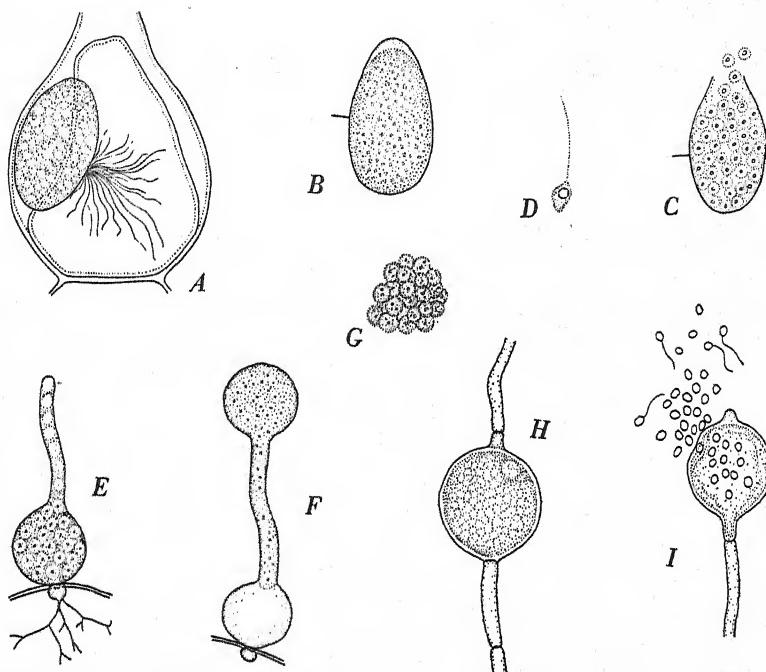


FIG. 41. Hypochytriaceae

A-D. Latrostium comprimens Zopf ($\times 200$) in oögonia of *Vaucheria*: *A*, sporangium within oögonium, resting on surface of egg of host; the delicate rhizoids are within egg; *B*, sporangium with large papilla laterally placed with respect to rhizoidal axis; *C*, discharging sporangium; *D*, anteriorly uniflagellate zoospore. *E-G. Rhizidiomyces apophysatus* Zopf (approx. $\times 400$) on oögonia of *Achlya*: *E*, mature apophysate sporangium with discharge tube; *F*, sporangium with contents emerging into vesicle formed at tip of discharge tube; *G*, mature zoospores formed outside sporangium. *H-I. Hypochytrium infestans* Zopf ($\times 540$) on ascocarp of *Helotium*: *H*, intercalary sporangium, showing discharge papilla; *I*, terminal apiculate sporangium discharging its anteriorly uniflagellate zoospores through a lateral pore.

(*A-D*, Zopf, 1894; *E-I*, Zopf, 1884)

anterior flagellum about 20μ long, formed in a vesicle produced at the tip of the discharge tube; resting spore not observed.

In soil, HAITI, VENEZUELA, MEXICO, JUGOSLAVIA.

The fungus was recovered on different types of bait, primarily

fruit-flies, in water cultures to which soil had been added. It was cultivated on agar but failed to form zoospores.

The species is of interest in that both chitin and cellulose walls are formed in the same organism.

RHIZIDIOMYCETES ICHNEUMON Gobi

Scripta Bot. Horti Univ. Imper. Petro., 15:251, pl. 6, figs. 1-28, pl. 7, figs. 29-39. 1900

Sporangium consisting of two intercommunicating parts, an epibiotic sessile spherical or rarely flattened portion 9-16 μ high, with a smooth thin colorless wall which collapses after zoospore discharge and a more or less elongate apical discharge tube, and (in previously uninfected host cells) a smaller endobiotic spherical, rarely pyriform or fusiform, portion 3-5 μ high, from the base of which emerges a system of delicate falsely dichotomously branched rhizoids; zoospores formed by progressive cleavage in an evanescent vesicle, from four to sixty, subspherical or ovoid, about 3 μ long, with fine or coarsely granular plasma and an anterior flagellum, movement slow and even.

Parasitic on actively moving and encysted *Chlamydomonas globulosa*, RUSSIA.

Because of the curious lack of a cross wall between the endo- and epibiotic parts the sporangium is a two-lobed structure. No cross walls were noted separating the rhizoids from the apophysis. In thalli forming on already infected cells of *Chlamydomonas* the rhizoids arose directly from the base of the epibiotic part, no apophysis being formed. This suggests that the apophysis possibly aided the immature parasite in maintaining its position on the moving host. With chloriodide of zinc the walls of the sporangium turned violet, the rhizoids, golden.

HYPHOCHYTRIUM ZOPF

Nova Acta Acad. Leop.-Carol., 47:187. 1884

(Figure 41 H-I, p. 481; Figure 42, p. 484)

Hypophagus (Zopf) Minden, Kryptogamenfl. Mark Brandenburg, 5:420. 1911 (1915).

Mycelium isodiametric, relatively broad, branched, extensive, with occasional cross walls, ramifying within the substratum; sporangia arising as terminal or intercalary swellings of the mycelium, from which they are cut off by cross walls; zoospores anteriorly uniflagel-

late, plasma without a prominent globule, either escaping fully or partly formed through a pore produced upon the deliquescence of a portion of the sporangium wall or cleaved out at the orifice of a discharge tube; resting spore not observed.

On fresh-water algae, ascocarps of Discomycetes, and moribund stems of maize.

Zopf's fungus was considered by Vuillemin (1907) to be a filamentous fungus parasitized by a chytrid. On this basis Minden placed it in a new genus, *Hyphophagus* of the Cladocytriaceae, retaining, however, the name Hypnochytaceae Schroeter for a family including *Macrochytrium*, *Zygochytrium*, and *Tetrachytrium*. No valid reason exists for the substitution of Minden's generic name for Zopf's, particularly since Valkanov (1929b) and Karling (1939b) have reaffirmed in related species Zopf's observations on the flagellation of the zoospore and ascertained that the sporangial and vegetative stages belong to the same organism.

KEY TO THE SPECIES OF HYPHOCYTRIUM

Vegetative system richly branched; in ascocarps of *Helotium*, in moribund tissues of maize, or in internodes of *Chara* and *Nitella*

Sporangium with an apiculus, discharging fully formed zoospores through a lateral pore; in *Helotium* *H. infestans*, p. 483

Sporangium without an apiculus, zoospores formed outside the sporangium, the protoplasmic mass discharged through a tube; in moribund tissue of maize and internodes of *Chara* and *Nitella* *H. catenoides*, p. 484

Vegetative system sparingly branched; in *Hydrodictyon*
H. Hydrodictii, p. 485

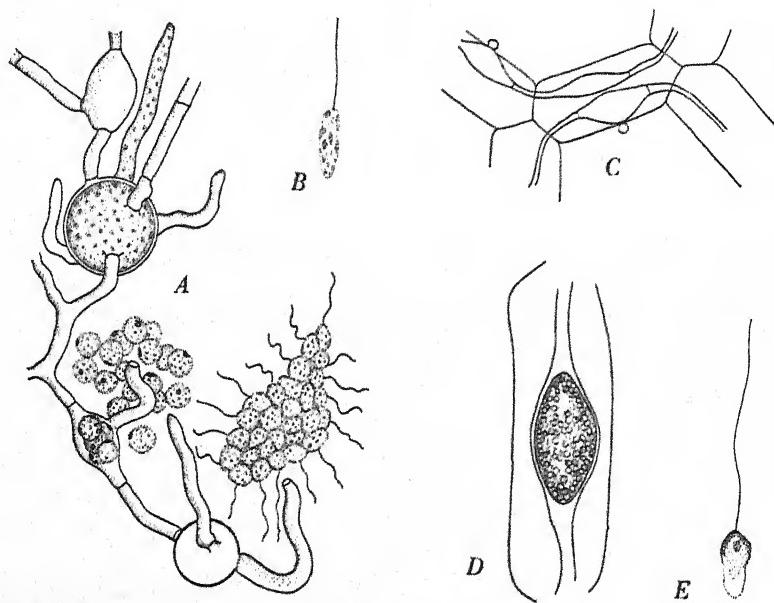
HYPHOCYTRIUM INFESTANS Zopf

Nova Acta Acad. Leop.-Carol., 47:187, pl. 18, figs. 13-20. 1884

(Figure 41 H-I, p. 481)

Hyphophagus infestans (Zopf) Minden, Kryptogamenfl. Mark Brandenburg, 5:420. 1911 (1915).

Vegetative system ramifying throughout the substratum, richly branched; sporangium, when intercalary, fusiform or ovoid, when terminal, spherical with a small apiculus, wall smooth, stout, colorless, collapsing after discharge; zoospores from sixty to one hundred in a sporangium, very small, spherical or ovoid, anterior flagellum

FIG. 42. *Hypochytrium*

A-B. Hypochytrium catenoides Karling on decaying maize: *A*, portion of thallus showing (lower right) formation of zoospores at orifice of discharge tube, group of quiescent spores, sporangium with its discharge tube, and (at top) empty segments from which contents have migrated; *B*, anteriorly uniflagellate zoospore. *C-E. Hypochytrium Hydrodictii* Valkanov in *Hydrodictyon*: *C*, parts of thalli in alga, showing epibiotic cysts of zoospore and primary and secondary swellings; *D*, resting spore; *E*, anteriorly uniflagellate zoospore.

(*A-B*, Karling, 1939b; *C-E*, Valkanov, 1929b)

fairly long, movement amoeboid, discharged with great speed from a lateral pore; resting spore not observed.

In ascocarp of a *Helotium*-like member of the Pezizaceae, on damp poplar stump, GERMANY.

HYPHOCHYTRIUM CATENOIDES Karling

Amer. J. Bot., 26:512-513, figs. 1-18. 1939

(Figure 42 A-B)

"Thallus predominantly polycentric and intramatrical; usually hyphal-like, and consisting of a linear series, up to 500 μ in extent,

of intercalary and terminal swellings and sporangia connected by tubular hyphae or isthmuses 1 to 138 μ in length and 2.2 to 4 μ in diameter; occasionally monocentric, oval, elongate, spherical and *Olpidium*-like. Zoosporangia terminal or intercalary, delimited by cross septa, hyaline, smooth, spherical, 10-35 μ , oval, 10 \times 12 μ -18-22 μ , broadly spindle-shaped 6 \times 10 μ -9 \times 18 μ , elongate and sometimes slightly irregular with 1-4 single or branched, straight, curved, coiled, or irregular exit tubes, 5-250 μ in length and 3-6 μ in diameter. Content of sporangium usually emerging as a naked spherical mass on the outside and undergoing cleavage into zoospores; occasionally undergoing complete or partial cleavage in the sporangium whereafter the segments glide out in succession. Zoospores anteriorly uniciliate, slightly flattened, oval, and elongate, 1.5 \times 3.5 μ -2 \times 3 μ , with several small, slightly refractive granules. Sexuality and resting spores unknown" (Karling, *loc. cit.*).

Weakly parasitic and saprophytic in *Zea mays*, *Nitella flexilis*, and *Chara coronata*, UNITED STATES.

HYPHOCHYTRIUM HYDRODICTII Valkanov

Arch. Protistenk., 67:122, figs. 1-11. 1929

(Figure 42 C-E)

Vegetative system arising as a lateral outgrowth from opposite sides of the rudiment of the sporangium, broad, tubular, not tapering, rarely branched, polyphagous; sporangia endobiotic, intercalary, from one to several (up to three) on the thallus, when single, sporangium formed from the primary swelling produced by the infecting zoospore, the cyst of which is persistent, when several, sporangia formed as well from secondary swellings of the vegetative system from which they are cut off by cross walls at maturity, broadly fusiform or occasionally somewhat irregular and gibbose, with a smooth, thin, colorless wall, forming a single functional papilla which pierces the host wall (rarely two or more nonfunctional papillae), method of opening not observed; zoospores ovoid with a broad, rounded apex, a single eccentric colorless globule, and a long anterior flagellum, capable of amoeboid motion, from fifty to one hundred or more in a sporangium, individual motion initiated within sporangium; resting spore terminal or intercalary, fusiform, with a thicker inner wall, contents charged with numerous droplets of uniform size, upon germination forming a single discharge papilla.

Parasitic on young cells of *Hydrodictyon reticulatum*, BULGARIA.

According to Valkanov, the development of the fungus is as follows: The zoospore, after coming to rest on the host wall and encysting, produces within the alga a spherical outgrowth which as it expands elongates parallel to the long axis of the *Hydrodictyon* cell (Fig. 42 C). This elongation usually takes place in opposite directions from the point of infection and results in the formation of a broad tubular hypha-like generally unbranched structure. The rudiment of the sporangium is recognizable from the beginning as the rather broad fusiform structure which was first laid down by the plasma of the penetrating zoospore and from opposite sides of which the vegetative system has emerged. Thus, as Valkanov has pointed out, the rudiment of the sporangium is laid down before the vegetative system. Other sporangia may be produced by secondary swellings of the "hyphae." It is probable that the primary structure absorbs host material in the same fashion as does a species of *Olpidium*, at least until the vegetative system is developed. Eventually the sporangial rudiment, which has grown more in thickness than in length, is cut off by cross walls from the rest of the thallus and one or more papillae are formed. The droplets within the contents coalesce to form the globules of the from fifty to one hundred zoospores into which the plasma is divided. The discharge of the already moving spores was not observed with certainty.

BIFLAGELLATAE

PLASMODIOPHORALES

ALTHOUGH the Plasmodiophorales are not ordinarily considered a primarily aquatic group of fungi, a survey of the species as listed in a monograph by Cook (1933b) reveals that over half are found as obligate parasites either of aquatic angiosperms or of lower aquatic plants. Very recently the discovery by Couch, Leitner, and Whiffen (1939) of a member of the order (*Octomyxa*) which parasitizes the water mold *Achlya* has stimulated considerable interest in the group among those concerned with purely aquatic organisms. The Plasmodiophorales have only of late been regarded as Phycomycetes (Gaumann, 1926; Gaumann and Dodge, 1928; Fitzpatrick, 1930¹). Previously they had been assigned either a vague intermediate position between Myxomycetes, Protozoa, and Phycomycetes or had been classed as a family of the Myxomycetes. Schroeter (1885, 1893) placed them in the Phytomyxinae, a group more animal-like than plantlike. Gaumann (*op. cit.*) thought them to be "Archimycetes," whereas Fitzpatrick included them in the order Chytridiales of the Phycomycetes (see Martin, 1932, 1940, for a more detailed discussion). Although it is apparent that the Plasmodiophorales can hardly be chytrids, their inclusion in the Phycomycetes seems justifiable. The recent work, mentioned above, of Couch, Leitner, and Whiffen on *Octomyxa* has made it quite evident that the genus *Woronina*, which together with *Olpidiopsis*, *Pseudolpidium*, and "Rozella" (sense of Fischer, not Cornu) made up the Woroninaceae, a family of the chytrids, should also be placed here.

Unfortunately, the whole group is so much in need of a thorough and careful biological and taxonomic study² that no account of any significance of the aquatic species can be given without considerable reinvestigation, in living material, of their developmental

¹ An excellent general discussion of the Plasmodiophoraceae may be found in this book.

² See Karling, *The Plasmodiophorales* (ix + 144 pp.; New York, 1942).

and morphological features. Particularly is this true of the fungi on aquatic flowering plants.

Two examples may be cited as illustrative of the confusion now prevalent with respect to essential developmental and morphological features of the phanerogamic parasites.¹ The first of these is concerned with the type of flagellation of the zoospore. Since this feature is considered of the greatest import in determining the relationships of aquatic Phycomycetes, it possesses unusual taxonomic significance. With perhaps one exception, all observers of the zoospores of species parasitic in phanerogams have described them as bearing a single anterior flagellum. This character, together with the so-called "plasmodial" nature of the thallus, lent strong support to the supposed relationship of these organisms to the Myxomycetes. Recent investigations by Ledingham (1939), however, have shown beyond question that the zoospores formed by species of *Plasmiodiophora*,² *Spongospora*, *Sorosphaera*, and *Polymyxa*—all, with the exception of the last-named, long-established genera of the order—possess two apically attached flagella of very different lengths. One of these, directed forward during motility, is very short, whereas the other, which trails behind the body, is considerably longer. Practically the same sort of zoospore is formed by the *Achlya* parasite, *Octomyxa*. Another feature of the zoospore is the strongly amoeboid changes of shape undergone at times by the spore body. Such a type of flagellation and such pronounced amoeboid activity by a swarmer are not features of the zoospores of typical biflagellate Phycomycetes. In this group, it will be recalled, the flagella are approximately of equal length and the shape of the body is relatively static. Neither can the swarmer with two unequal flagella be considered typically myxomycetous, although biflagellate types are occasionally found (Sinoto and Yuasa, 1934; Yuasa, 1935).

The second example of the prevailing confusion deals with the life history. Cook (1933b) states in his monograph that, typically,

¹ No attempt has been made to include here a summary of the extensive literature of these fungi. See Cook (1933b).

² A careful perusal of the paper on *Plasmiodiophora Brassicæ* by Cook and Schwartz (1930) reveals that the anteriorly uniflagellate swarmers described as the "swarm spores" were found in Knopf's solution to which glucose had been added. In this solution resting spores—necessarily contaminated—had been placed for germination. No actual emergence of the swarmer from the cyst was ever observed. Furthermore, the authors were by no means certain of the method of locomotion of the zoospores formed in the ephemeral zoosporangia (gametangia?).

the sequence of development is as follows: Each of the thick-walled spores, which are formed in abundance in host plants, produces upon germination an anteriorly uniflagellate swarm cell. These swarmers fuse in pairs, and the resulting biflagellate body, with its single fusion nucleus, penetrates the new host plant, where it becomes multinucleate and where it may migrate to a place favorable for further development. It then undergoes a series of simultaneous nuclear divisions of the peculiar protomitotic type,¹ by which a large number of nuclei are formed. At this stage the vegetative body is an unwalled multinucleate thallus, termed the "plasmodium," or "myxamoeba," which feeds upon the host contents. At maturity the stainable chromatin of the nuclei is extruded into the cytoplasm. This has been termed the "akaryote stage." Subsequently the chromatin returns to the nuclei, which then divide twice, halving the number of chromosomes (not observable as separate objects in promitotic divisions) at the first division. The second division is homotypic. Cleavage furrows then laid down in the cytoplasm around each of the nuclei of the thallus define clusters of resting spores. It is on the method of formation and the type of aggregation of these resting spores that the present criteria for genera are established. In *Sorosphaera* and *Sorodiscus*, the "spore ball" or "spore cake," that is, the mass of resting spores formed from a single thallus, is surrounded by a common wall laid down during resting-spore formation. In *Plasmodiophora*, *Spongospora*, *Tetramyxa*, *Ligniera*, *Polymyxa*, and *Octomyxa*, no such common wall occurs. Cook mentions the appearance in *Plasmodiophora* and *Ligniera* of a second type of reproductive body, a zoosporangium, but he does not attempt to interpolate it in the life history. The evidence for the fusion of zoospores in *Plasmodiophora Brassicae* (Cook and Schwartz, 1930) is apparently purely circumstantial (see p. 488, note 2).

The recent studies of Ledingham (1939) on *Polymyxa graminis* have led him to lay considerable emphasis on the sporangial stage, passed over so lightly by Cook. Even here, the precise connection between the resting stage, which in *Polymyxa* developed in essentially the manner described by Cook (see above), and the sporangial stage has not been established by direct observation. Ledingham, however, gives abundant evidence to indicate that they are, indeed, phases of the same organism. If wheat plants are grown in sterilized

¹ See Nawaschin (1899) and Horne (1930).

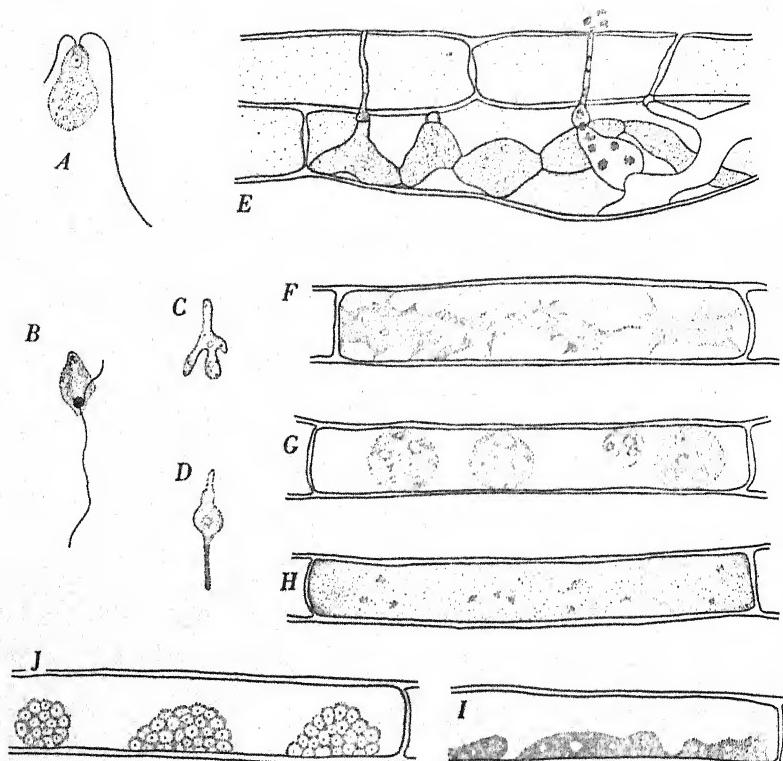


FIG. 43. *Polymyxa graminis* Ledingham in roots of wheat

A. Free-swimming zoospore with a long and a short flagellum, both of which are here directed anteriorly. B. Zoospore immediately after release. C-D. Shapes assumed by zoospores during amoeboid movement; flagella have now been lost. E. Septate thalli, some segments of which have become converted into zoosporangia; each sporangium bears a discharge tube which reaches the outside medium. F. Naked myxamoebae during active vegetative growth; it is in such thalli that the nuclei divide by protomitosis. G. Meronts formed by division of myxamoebae. H. Same meronts coalesced. I. Myxamoebae just prior to segmentation into resting spores. J. Spore clusters beginning to be formed from myxamoebae. (A-B, $\times 1300$; C-D, $\times 750$; E-J, $\times 450$.)

(Ledingham, 1939)

soil which has been inoculated with finely pulverized roots containing resting spores of *Polymyxa*, great numbers of thin-walled, septate, multinucleate thalli, which even in their youngest stages are sur-

rounded by a delicate wall, develop in the roots. At maturity each of these segments becomes converted into a zoosporangium that is provided with a discharge tube (Fig. 43 E). This tube eventually reaches the exterior, and through it numerous biflagellate zoospores (Fig. 43 A-D), exactly like those produced at the germination of the resting spore, are discharged. Their further fate could not be determined, although the evidence indicated that they penetrate the host cell. A few resting spores are formed early in the course of the infection, but by far the greater number are produced somewhat later, when the roots are very heavily diseased. The plasmodium which eventually produces the resting spores is unwalled, in contrast to that forming the zoosporangia. As it grows and becomes multinucleate by protomitosis it gives rise to long radiating threadlike pseudopodia, which may be retracted after a time (Fig. 43 F). The thallus then may fragment into a group of secondary thalli or "meronts" (Fig. 43 G). Occasionally, fusion of distinct plasmodia occurring in the same host cell was observed (Fig. 43 H). It could not be determined whether these plasmodia were meronts derived from the same or from different thalli. As the plasmodium matures, its contents become denser (Fig. 43 I), lines of cleavage form around each nucleus, and the walls of the resting spores are laid down (Fig. 43 J). Investigations of the nuclear condition in the maturing thallus before resting-spore formation indicated that the akaryote stage mentioned in Cook's account was recognizable. By the use of certain stains (Newton's iodine-gentian-violet) it could be demonstrated, however, that the chromatin was not, in fact, extruded, but that it merely failed to react to the usual stain (iron-alum haematoxylin). No nuclear fusions, as reported by Webb (1935) in *Sorosphaera* were observed. Just previously to cleavage of the cytoplasm ordinary division figures (not of the promitotic type) were formed, but whether meiosis took place could not be determined.

From Ledingham's account it is evident that he regards the formation of the thin-walled zoosporangia as an essential and integral part of the life history of *Polymyxa*. He also intimates that they precede the production of resting spores. He further shows from his own studies on *Polymyxa* and *Spongospora* and from those of Cook (1926) and Cook and Schwartz (1930) on *Ligniera* and *Plasmodiophora* that differences in the zoosporangial stages of these genera are well marked and may, in fact, prove of greater taxonomic worth than the somewhat unsatisfactory character now used, namely, the method

of aggregation of the resting spores (Palm and Burke, 1933; Wernham, 1935). It is interesting to note that though Cook discovered the sporangial stage and mentions it in the discussion of those species in which it occurs, he makes little taxonomic use of it; nor, as has been noted, does he attempt to interpolate it in the life cycle of the Plasmodiophoraceae.

The uncertain and confused state of our knowledge of the life cycle may be illustrated by two investigations, both dealing with *Plasmodiophora Brassicae* (P. M. Jones, 1928; Cook and Schwartz, 1930). The cycle proposed by P. M. Jones involves the formation of two kinds of gametes, large and small. These conjugate in pairs, the fusing gametes being alike in size (that is, small fuse with small, large with large). Two different cycles ensue, one outside, the other inside the host. Other features described are the "budding" of the plasmodium, the formation of several types of cysts, and so on. The reader is referred to Jones's paper for further details of this highly aberrant life cycle. Cook and Schwartz believe that the swarmer emerging from the cyst (resting spore) enters the root hair and that the resultant thallus becomes converted into a small somewhat spherical zoosporangium. The "zoospores" from this zoosporangium after discharge conjugate in pairs, probably after entering the host. This conjugation apparently rests on purely indirect evidence. The presumably diploid thallus then forms the "plasmodium" and, subsequently, the resting spores, after what is possibly a reduction division.

From the somewhat controversial nature of this discussion it can be seen that much investigation on the already established species of the group will be necessary before sure taxonomic criteria can be set up. In this connection the recent discovery by Couch, Leitner, and Whiffen (1939) of the plasmodiophoraceous parasite of *Achlya glomerata*, already mentioned, is of interest from several points of view. They summarize their findings on *Octomyxa* as follows:

The species is an obligate parasite on the hyphae of *Achlya glomerata*, causing the formation of gall-like swellings on the hyphal ends. Infection is by single spores which enter the hyphae without leaving a cyst. The spore is carried to the hyphal tip where it develops into a multinucleate plasmodium. Vegetative nuclear divisions are of the protomitotic type characteristic of the Plasmodiophoraceae. The early formed plasmodia develop into sori of zoosporangia, which in turn give rise to zoospores. The zoospores

are biciliate with one long and one short cilium. The later formed plasmodia form sori of resting spores. These are found as a rule in groups of eight, each group being made up of two tetrads of resting spores.

These investigators reach a conclusion of greatest interest with respect to the near affinities of *Octomyxa*, namely, that it is closely related to *Woronina polycystis* Cornu, in the sense of Fischer (1882). This is wholly in accordance with the conclusion of the present author that *Woronina*, rather than being a chytrid, is actually closely allied to the Plasmodiophorales. Earlier, Winge (1913) was of a similar opinion.

The naked plasma of the parasite *Woronina* may be particularly difficult to distinguish in the turbid contents of the host cell. Fischer (1882) observed in the probably closely allied "*Rozella septigena*" that the very young thallus was entirely lost to view, and conjectured that the plasma of host and parasite actually mingled to form a "plasmodium." The question as to whether or not a true plasmodium is formed is an interesting one, since it has been presumed in the past to be indicative of a primitive type of vegetative thallus. Actually, thalli devoid of specialized vegetative structures are formed in true chytrids (Olpidiaceae, Synchytriaceae) as well as in the Plasmodiophoraceae. Butler (1907) thinks that in *Woronina* and *Rozella septigena* a true plasmodium is sometimes formed and cites Plate 2, Figure 12, and Plate 3, Figure 26, of Fischer (1882) as lending strong support to his view. In the first of these figures numerous zoospores of *Woronina polycystis* may be seen to have successfully infected a hyphal tip. Subsequently there are formed within the host two groups of sporangia sori separated by a cross wall. In the second figure a gemma of the host infected by many zoospores of *Rozella septigena* has formed within it at maturity only four walled-off outgrowths, each of which contains a single spiny resting spore. Though these examples lend strong support to Butler's idea that thalli actually fuse to form a plasmodial structure, they are not absolutely conclusive, and the possibility that one or two thalli may gain the ascendancy at the expense of the others cannot be overlooked. Obviously, cytological as well as morphological evidence will be necessary to settle this question with finality. In *Woronina polycystis* the host, by the formation of transverse septa, walls off the body of the parasite as it increases in size; this may be for the protection of the healthy parts. The thallus continues to absorb the host contents,

fills the lumen, and, according to Cook and Nicholson (1933), becomes surrounded by a cellulose wall after segmentation. Dangeard (1890-91b) reports that the cytoplasm of the thallus forms a dense parietal layer lining a central vacuolar cavity. In this parietal layer numerous small nuclei are found, frequently elongated in the direction of the long axis of the host filament. They often appear to be composed of a simple mass of chromatin. In some, however, the chromatic material seems to be surrounded by a clear zone, as if it were really nucleolar in nature. *Rozella septigena* also was studied cytologically by Dangeard (*op. cit.*). He describes the vegetative stage as similar to that of *Woronina*, though the nuclei are larger, having a large spherical or angular deeply staining nucleolus surrounded by hyaloplasm and a nuclear membrane. In some walled-off thalli up to twelve nuclei were found near the center, apparently having been formed amitotically. More frequently the nuclei were regularly dispersed in the dense cytoplasm. The lack of mitotic figures in both *Woronina* and *Rozella septigena* does not necessarily prove that division of the nucleus is amitotic. More extensive studies may show that, actually, mitosis or protomitosis prevails.

In *Woronina* the contents of the thallus fragment simultaneously, or nearly so, to form either a group of from two to six nucleate spherical sporangia or aggregates of thick-walled angular resting cysts. Cook and Nicholson (1933) describe the multinucleate thallus as becoming furrowed, cellulin being laid down in the furrows to delimit the numerous spherical sporangia. The zoosporangia are thin-walled, separate, usually spherical bodies, which may sometimes be formed in great numbers in the host cell. At maturity each sporangium produces a short papilla, which pierces the wall of the host. The sporangial contents become cleaved into a varying number of small zoospores; these escape through a short tube upon the dissolution of the tip of the papilla. The zoospores, according to the description and figures of Fischer (1882), are narrowly ellipsoidal, with an anteriorly attached forwardly directed flagellum and a laterally attached, somewhat longer, posteriorly directed one. Cook and Nicholson, on the other hand, describe and figure the zoospore as spherical, with two apically attached posteriorly directed flagella of approximately the same length. A small granule is found in the body. After a swarm period these zoospores encyst on the host wall and

produce a delicate infection tube, through which their contents are carried inside the host. The resting stage is formed from a vegetative thallus, which, so far as is now known, does not differ in origin or structure from that which produces the sorus of sporangia. The contents of the thallus become divided at maturity into an ovoid or irregularly shaped mass of thick-walled, angular, and, according to Cook and Nicholson, uninucleate resting spores. These groups, or "cystosori," appear in every way comparable with the groups of resting spores found in *Ligniera*, *Spongospora*, and so on. They are not surrounded by a common soral membrane. At germination the angular cysts become rounded and expand, each being converted into a zoosporangium (Fischer, 1882). No sexuality has thus far been demonstrated in *Woronina*. It seems logical to suppose, however, that if it occurs a fusion of gametes will be found and that this fusion probably takes place before the formation of the thallus which gives rise to the cystosorus.

SYSTEMATIC ACCOUNT

PLASMODIOPHORALES

MICROSCOPIC parasitic aquatic or semiaquatic fungi, frequently producing hypertrophy of the host; the thallus endobiotic, holocarpic, without specialized vegetative structures, naked and more or less amoeboid or surrounded by a delicate wall, sometimes dividing into several daughter thalli (meronts, schizonts), the membranated thallus forming at maturity one or more thin-walled zoosporangia (gametangia?), the unwalled thallus becoming fragmented into a cluster or aggregation of thick-walled resting spores which produce zoospores at germination; zoospores biflagellate (always?), with one long posteriorly directed flagellum and a short anteriorly directed one; sexuality, in species in which it is known, by fusion of motile amoeboid or biflagellated isogamous gametes, the zygote becoming a naked thallus, which at maturity forms the resting spores.

This order contains only one family, the Plasmodiophoraceae, parasites of terrestrial and aquatic flowering plants and fresh-water algae, Phycomycetes, and Isoetes.

PLASMODIOPHORACEAE¹

Characters those of the order.

As here understood the Plasmodiophoraceae include *Woronina*, which had been placed by Minden (1915) and later authors in the Woroninaceae. *Rozella septigena*, in the sense of Fischer (1892), and *R. simulans* (see p. 126) may possibly be referable to the Plasmodiophoraceae (see the zoospores of *R. septigena* figured by Tokunaga, 1933a).

For the reasons mentioned above (p. 487), no original taxonomic treatment of the genera and species of the parasites of aquatic angiosperms can be attempted. The reader is referred to the monograph by Cook (1933b) for details of these and other species.

KEY TO THE AQUATIC GENERA OF THE PLASMODIOPHORACEAE

Parasitic in the hyphae of aquatic Phycomycetes and in filaments of

Vauheria; zoosporangia globose

Infected parts of the host segregated by cross walls; resting spores either linearly or irregularly grouped or aggregated to form a somewhat globose mass WORONINA, p. 497

Infected parts of the host not segregated by cross walls; resting spores grouped predominantly in eights OCTOMYXA, p. 501

Parasitic in aquatic angiosperms, *Isoetes*, and *Chara*; zoosporangia variously shaped

Aggregation of resting spores free, not surrounded by a common soral membrane

Resting spores scattered, without definite arrangement in the host cells; infected parts of the host strongly hypertrophied

PLASMODIOPHORA, p. 502

Resting spores more definitely aggregated; infected parts of the host with or without hypertrophy

Resting spores in irregular groups; host not hypertrophied

LIGNIERA, p. 503

Resting spores in groups of two and four; host hypertrophied

TETRAMYXA, p. 505

Aggregation of resting spores surrounded by a common soral membrane, the spores in two layers, forming a flat ellipsoidal plate

SORODISCUS, p. 506

¹See also Karling, as cited on p. 487, note 2.

WORONINA CORNU

Ann. Sci. Nat. Bot., V, 15:176. 1872

(Figure 44 A-E, p. 499)

Thallus unwalled, endobiotic, holocarpic, in walled-off portions of the host (the walls those of the host), forming the rudiment of the sporangia sorus or cystosorus; sporangia grouped, each forming a pore through which the biflagellate zoospores emerge; cysts thick-walled, angular or spherical, generally closely aggregated into cystosori, each upon germination functioning as a zoosporangium.

Parasites of other Phycomycetes and green algae.

The genus is very animal-like in some of its features. If Zopf's observations on the behavior of the plasmodium in *Woronina glomerata* are unquestionably confirmed and extended the species will provide a remarkable connecting link with *Proteomyxa*-like protozoa.

The best-known species, *Woronina polycystis*, is a common parasite in *Saprolegnia* and *Achlya*. The observations of Fischer (1882) indicated that the linear sequence of thallus development found in heavily infected hyphae was not due to successive fractionation of a single thallus but to multiple infection. A single zoospore gave rise to a single thallus and the transverse septa were formed by the host, not the parasite. Cook and Nicholson (1933), on the other hand, declare that the multinucleate "plasmodium" may, at the time of septation by the host, be divided and that the segments produced may develop into full-sized thalli. In this manner a series of plasmodia may be formed. They also noted that the thallus feeds mainly upon the globules of oil present in the host cells.

KEY TO THE SPECIES OF WORONINA

- Parasitic in aquatic Phycomycetes; resting spores in compact masses
or separate
- Cystosorus composed of globular compact masses of angular rest-
ing spores *W. polycystis*, p. 498
- Cystosorus composed of linear groups of unconnected spiny rest-
ing spores *W. asterina*, p. 498
- Parasitic in fresh-water algae; the resting spores separate, in linear
groups *W. glomerata*, p. 500

WORONINA POLCYSTIS Cornu

Ann. Sci. Nat. Bot., V, 15:176, pl. 7. 1872

(Figure 44 A-C)

Sporangia sorus terminal or intercalary in segments (often swollen) of the host, sometimes in linear series, the segments up to 476 μ long by 60 μ in diameter; sporangia varying in number according to the size of the sorus, spherical, 14–16 μ in diameter, wall thin, smooth, colorless, with a short discharge papilla; zoospores biflagellate, 3–4 μ long by 2 μ wide, emerging through a pore formed upon the dissolution of the papilla; cystosorus borne like the sporangia sorus, dark, variable in size and shape, predominantly somewhat ovoid or ellipsoidal or linear; cysts (cystosporangia) thick-walled, 4–8 μ wide, somewhat angular, each upon germination becoming more spherical, longer, thin-walled, and functioning as a zoosporangium.

Parasitic in *Achlya polyandra*, *A. racemosa*, *Saprolegnia spiralis*, *Cornu* (*loc. cit.*), *Achlya sp.*, *S. monoica*, Dangeard (1890–91b:86, pl. 4, figs. 1–4), FRANCE; *Saprolegnia sp.*, Fischer (1882), Minden (1915:275), GERMANY; *Achlya racemosa*, Sorokin (1883:39, fig. 51), EUROPEAN RUSSIA, ASIATIC RUSSIA; *Saprolegnia sp.*, Maurizio (1895), SWITZERLAND; *Saprolegnia sp.*, *Achlya sp.*, H. E. Petersen (1909:425; 1910:556, fig. 27 a-b), DENMARK; *Achlya sp.*, *Saprolegnia sp.*, Cook and Nicholson (1933:851, figs. 1–16), host (?), Forbes (1935b), *Achlya spp.*, Sparrow (1936a:425), ENGLAND; *Achlya spp.*, Sparrow (1933c:515), UNITED STATES.

The fungus in *Oedogonium sp.* referred by Cook (1932a:133, figs. 1–6) to this species cannot be identified with it.

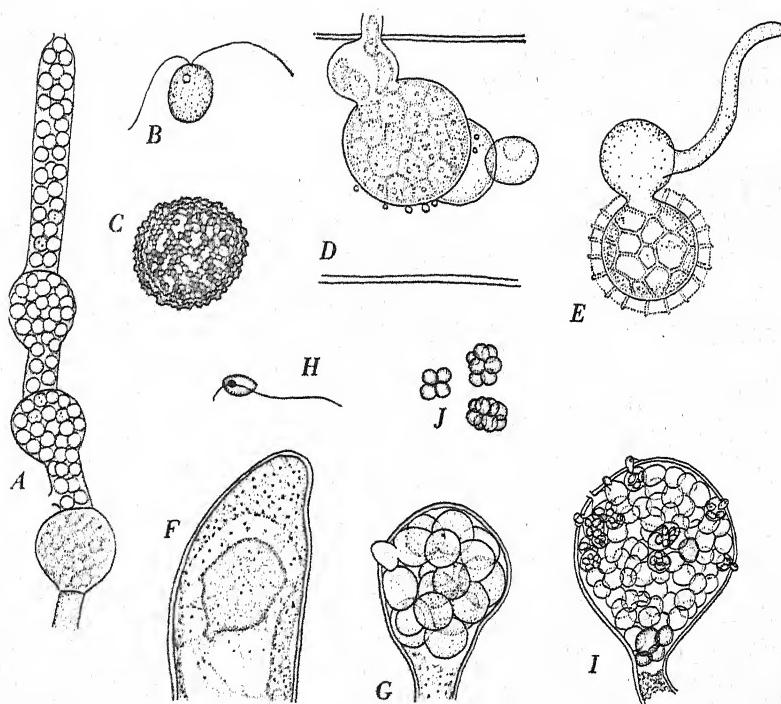
Cook and Nicholson (*loc. cit.*) describe the zoospores as spherical and the resting cysts as oval or ellipsoid. Fischer states that the zoospores are elongate, often flattened on one side, and that the cysts are polygonal.

The fungus with posteriorly uniflagellate zoospores described by Pringsheim (1860:205, pl. 23, figs. 1–5) and commonly ascribed to this species, has been placed in a new genus, *Pringsheimiella* (see p. 108), by Couch (1939b).

WORONINA ASTERINA Tokunaga

Trans. Sapporo Nat. Hist. Soc., 13:26, pl. 2, figs. 15–16. 1933

Sporangia sorus linear, 96–216 μ long by 18–30 μ in diameter; zoosporangia 4–20, in one or two rows, spherical, 12–19 μ in diameter,

FIG. 44. *Woronina* and *Octomyxa*

A-C. Woronina polycystis Cornu in Saprolegniaceae: *A*, portion of hypha of *Achlya* ($\times 110$); most of the many spherical sporangia in upper part have discharged their zoospores; in basal segment sporangia are just beginning to form; *B*, interpretation of zoospore ($\times 1600$) according to Cook and Nicholson (1933); *C*, cystosorus of small angular resting spores ($\times 170$). *D-E. Woronina glomerata* (Cornu) Fischer ($\times 690$) in *Vaucheria*: *D*, zoosporangium discharging its zoospores through tube opening to outside of alga; *E*, germinating resting spore on which discharge tube has been formed. *F-J. Octomyxa Achlyae* Couch, Leitner, and Whiffen in *Achlya*: *F*, thallus of parasite ($\times 500$) in tip of host hypha; *G*, group of nearly mature zoosporangia ($\times 650$); *H*, zoospore bearing short anterior flagellum and long posterior one ($\times 1000$); *I*, hypertrophied tip of host hypha bearing numerous zoosporangia ($\times 315$), some of which are discharging their zoospores; *J*, several groups of resting spores ($\times 500$), which, like the sporangia, are formed in great numbers in swollen hyphal tips.

(*B*, Cook and Nicholson, 1933; *C*, Cornu, 1872a; *D-E*, after Zopf, 1894; *F-J*, Couch, Leitner, and Whiffen, 1939)

with a thin smooth colorless wall and a short papilla; zoospores spherical or ovoid, 3–4 μ in diameter; cystosorus like the sporangia sorus in size and shape, cysts spherical, 12–22 μ in diameter, golden, the thick wall covered with large conical spines, germination not observed.

Parasitic in hyphae of *Achlya americana*, JAPAN.

WORONINA GLOMERATA (Cornu) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):67. 1892

(Figure 44 D-E, p. 499)

Chytridium glomeratum Cornu, Ann. Sci. Nat. Bot., V, 15:187, pl. 7, figs. 20–22. 1872.

Sporangia sorus cylindrical, variable in size, 70–300 μ long by 50–96 μ in diameter; sporangia varying in number, spherical, 10–33 μ in diameter, with a smooth colorless wall and a narrow discharge tube, zoospores ellipsoidal to cylindrical, 3.6 \times 2.4 μ , biflagellate; cystosorus borne like the sporangia sorus, cysts spherical or ellipsoidal, 12–22 μ in diameter, thick-walled, the outer wall reticulate with minute spines, upon germination forming a flasklike tube which pierces the algal wall and through which the zoospores presumably escape.

Parasitic in *Vaucheria terrestris*, *V. sessilis*, Cornu (*loc. cit.*), FRANCE; *Vaucheria terrestris*, *V. sessilis*, Zopf (1894:43, pl. 2, pl. 3, figs. 1–3), Minden (1915:275), GERMANY; *Vaucheria sessilis*, Voronichin (1920:10), RUSSIA; *Vaucheria sp.*, Valkanov (1931a:361), BULGARIA; *Vaucheria sessilis*, Tokunaga (1933a:26, pl. 2, figs. 17–18), JAPAN.

On the basis of Zopf's observations on the vegetative stage this curious organism seems more animal-like than fungoid. According to Zopf, the swarmer from the overwintering spore penetrates the *Vaucheria* filament in early spring and, once inside, becomes amoeboid. The amoebae feed upon the chlorophyll of the host—ingesting it as solid particles into the plasma—increase in size, and sometimes fuse together to form an extensive netlike plasmodium. After the plasmodium has fragmented the chlorophyll residue is expelled and each of the fragments rounds off, surrounds itself with a thin wall, and forms a sporangium. In each sporangium, zoospores are produced which are discharged through a tube into the water, thus spreading the infection. Upon the advent of unfavorable conditions

later in the season the plasmodium, which may be so large as to fill the whole algal tube, divides into segments ("Teilplasmodium") and from each of these is formed a sorus of cysts.

It is important that observations be made on the method of infection. If this occurs by encystment and by the formation of a penetration tube, relationship with *Woronina* is strengthened; if the swarmer enters as a whole, without encystment, its animal-like nature is further emphasized.

The imperfectly known *Woronina aggregata* Zopf (*op. cit.*, p. 60) in *Mougeotia* has a round cluster of from ten to twenty spore cysts which discharge their zoospores through a tube. No resting spores were observed. Here, as in *W. glomerata*, the plasmodium ingests the chlorophyll and starch and expels material before encysting. What is probably another species is mentioned by Zopf as occurring in *Pilobolus*.

IMPERFECTLY KNOWN SPECIES OF WORONINA

? *Woronina elegans* (Perroncito) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):66. 1892

Chytridium elegans Perroncito, Centralbl. f. Bakteriol., Parasitenk. u. Infektionskrankh., Abt. 2, 4:295. 1888.

Sporangia sorus spherical or somewhat stellate, filling the body cavity of the animal, 60–110 μ in diameter, with rose-red contents; sporangia 8–20 or more, spherical or pyriform, 20–30 μ in diameter, discharge tube 5–100 μ or more long by 3–4 μ in diameter; zoospores 30–50, ovoid, reddish, 4–5 μ long by 2–3 μ thick, with two long oppositely directed flagella.

Parasitic in adults and eggs of *Philodina roseola*, in a thermal spring, ITALY.

From the color of the zoospores it appears possible that here, as in *Woronina glomerata*, solid particles are ingested.

OCTOMYXA COUCH, LEITNER, AND WHIFFEN

J. Elisha Mitchell Sci. Soc., 55:400. 1939

(Figure 44 F–J, p. 499)

"Parasitic on Achlya causing hypertrophy of host. The infecting zoospore giving rise to a naked protoplast, which at maturity forms a large spherical sorus of zoosporangia or resting spores. Vege-

tative nuclear divisions of the 'cruciform type.' Zoosporangia thin-walled, spherical, ovoid, or slightly flattened by pressure, zoospores with one long and one short flagellum. Resting spores spherical and with a slightly thickened wall; aggregated in groups of eight, each group not enclosed in a common membrane" (Couch, Leitner, and Whiffen, *loc. cit.*).

Parasitic in *Achlya*.

OCTOMYXA ACHLYAE Couch, Leitner, and Whiffen

J. Elisha Mitchell Sci. Soc., 55:400, pls. 47-48. 1939

"Obligate parasite on *Achlya glomerata* Coker, causing spherical galls mostly on ends of hyphae. Galls 50-150 μ thick. Plasmodium at maturity partially or completely filling the gall and segmenting into either zoosporangia or resting spores. Zoosporangia globose to ovoid, thin-walled, variable in size, 6 μ to 16 μ thick. Spores discharged through small papillae which are formed only on some of the sporangia next to the host wall, the other peripheral sporangia as well as those deeper within the sorus discharging their spores through the peripheral ones; zoospores biciliate with one long posterior and one short anterior flagellum, 6-14 in a zoosporangium. Resting spores smooth-walled, 2.4 μ to 3.2 μ , aggregated in groups of eight. Sporangial and resting spore membranes without cellulose as shown by a negative reaction with chlor-iodide of zinc" (Couch, Leitner, and Whiffen, *loc. cit.*).

Parasitic in *Achlya glomerata*, coll. F. Foust, UNITED STATES.

PLASMODIOPHORA Woronin

Arbeit. St. Petersburg Naturf. Gesell., 8:169. 1877; Jahrb. wiss. Bot., 11:548.
1878

Ostenfeldiella Ferdinandse and Winge, Ann. Bot. London, 28: 648. 1914.

"Spores not aggregated together into a spore-ball or spore-cake nor enclosed in a common membrane. Myxamoebae generally large, completely filling the host cell. When mature, myxamoebae producing a large number of spores. Spores on germination each producing a single swarm cell which reinfects the host. Conjugation occurring between swarm cells outside the host plant. Reduction division taking place between the akaryote stage and the formation

of spores. The organisms cause hypertrophy of the host tissues" (Cook, 1933b).

Parasites of terrestrial and aquatic angiosperms.

PLASMODIOPHORA DIPLANTHÉRAE (Ferdinansen and Winge) Cook¹

Hong Kong Naturalist (Suppl.), No. 1:34. 1932; Arch. Protistenk., 80:194,
text fig. 9, pl. 6, figs. 5-6. 1933

Ostenfeldiella Diplantherae Ferdinansen and Winge, Ann. Bot. London, 28:648, text figs. 1, 4, pl. 45. 1914.

"Spores spherical, brown, 4-4.5 μ in diameter, with thin, hyaline, smooth membranes. Spores producing myxamoebae which grow to a large size, 125-200 μ in diameter, containing many nuclei. Myxamoebae forming spores within the host cells which increase in size from 35 μ to 200 μ in diameter" (Cook, *loc. cit.*).

Parasitic in *Diplanthera Wrightii*, causing swelling of the internodes, ST. CROIX, VIRGIN ISLANDS.

LIGNIERA MAIRE AND TISON

C. R. Acad. Sci. Paris, 152:206. 1911

"Spores not aggregated together into a spore ball or spore cake, nor enclosed in a common membrane. Myxamoebae small, completely filling the host cells. When mature, myxamoebae producing both spores and zoosporangia. Zoosporangia on germination producing zoospores. Spores on germination producing swarm cells. Conjugation occurring between swarm spores and zoospores respectively. Reduction division taking place prior to spore and zoospore formation. The organisms cause no hypertrophy of the host tissue" (Cook, 1933b).

In roots of aquatic and marsh plants.

¹ See also *Plasmodiophora bicaudata* Feldmann (*Bull. Soc. Hist. Nat. Africa du Nord*, 31:171-177, 2 figs. 1940), in *Zostera nana*. *P. Halophilae* Ferdinansen and Winge (*Centralbl. f. Bakteriol., Parasitenk. u. Infektionskrankh.*, Abt. 2, 37:167, 3 figs. 1913), causing galls on petioles of *Halophila ovalis*, a marine angiosperm growing near Java, is considered by Cook to be an imperfectly known species. Judging only from the meager description and figures, it can probably be referred to this order. Possibly the same parasite has been found in the West Indies by Feldmann (*Bull. Soc. Bot. France*, 83:608. 1936).

LIGNIERA JUNCI (Schwartz) Maire and Tison

C. R. Acad. Sci. Paris, 152:206. 1910

Sorosphaera Junci Schwartz, Ann. Bot. London, 24:236, 511. 1910.*Sorosphaera graminis* Schwartz, *ibid.*, 25:791, pl. 61. 1911.*Ligniera radicalis* Maire and Tison, C. R. Acad. Sci. Paris, 152:206. 1911.*Sorolpidium Betae* Němec, pro parte, Bull. Internat. Acad. Sci. Bohême, 16:136. 1911.*Ligniera Bellidis* Schwartz, Ann. Bot. London, 28:232, pl. 12, figs. 7-8. 1914.*Ligniera Menthae* Schwartz, *ibid.*, p. 232, pl. 12, figs. 1-6.*Ligniera Alismatis* Schwartz, *ibid.*, p. 233.*Anisomyxa Plantaginis* Němec, pro parte, Bull. Internat. Acad. Sci. Bohême, 18:18. 1916.*Ligniera pilorum* Fron and Gaillat, Bull. Soc. Mycol. France, 41:390, pl. 10. 1925.

"Spores spherical, 4-7 μ diam., with thin hyaline walls. Zoosporangia subglobose, 15-20 μ diam., giving rise to zoospores, 4.5 μ long by 3.5 μ diam. Spores germinating to produce swarm cells. Both zoospores and swarm cells producing amoebae which become myxamoebae. Schizont formation does not occur. Meiosis occurring immediately before spore formation, or after the formation of zoosporangia. The fungus causes no hypertrophy of the host tissue . . ." (Cook, 1933b).

Parasitic in both terrestrial and aquatic plants. It is recorded in the following hosts by Cook: *Alisma plantago*, *Callitricha stagnalis*, ? *Isoetes lacustris*, *Polygonum Hydropiper*, *Potamogeton natans*, *Ranunculus aquatilis*, *R. circinatus*, *Veronica Beccabunga*. Other host plants listed by Cook are: *Bellis perennis*, *Cerastium vulgatum*, *Chrysanthemum leucanthemum*, *Iris pseudoacorus*, *Juncus articulatus*, *J. bufonius*, *J. lamprocarpus*, *J. obtusiflorus*, *Mentha Pulegium*, *Plantago major*, *Poa annua*. ENGLAND, FRANCE, GERMANY.

The synonymy is that given by Cook. It should be noted that although Cook discusses *Ligniera Isoetes* Palm (1918) and lists *Isoetes* as a host, it does not appear in the synonymy. Furthermore, since Schwartz (*op. cit.*, p. 232) refers to his *Sorosphaera graminis* as *L. graminis*, this binomial should, it would seem, also be included in the synonymy. The combination was made by Winge (1913:15).

Lastly, Cook cites himself as the author of the combination *L. Junci*, whereas it was made in 1911 by Maire and Tison. *L. Isoetes* has been reported as occurring in New Jersey by Karling (1934c).

TETRAMYXA GOEBEL

Flora, 67:517. 1884

(Figure 45 G, p. 506)

Thecaphora Setchell, Mycologia, 16:243. 1924.

"Spores aggregated in groups of four, not enclosed in a common membrane but free and frequently becoming separated from one another. Spores spherical with smooth walls. Spores on germination giving rise to swarm cells which eventually reinfect the host tissue. Infection taking place through the cells of the gall and through the exterior as well. Meiosis occurring before spore formation. The organisms cause hypertrophy of the host tissue" (Cook, 1933b).

Parasitic on marine angiosperms.

TETRAMYXA PARASITICA Goebel

Flora, 67:517, pl. 7. 1884

Thecaphora Ruppiiæ Setchell, Mycologia, 16:243, pl. 18, figs. 3-4. 1924.

"Spores spherical 3.5 μ diam., on germination producing swarm cells which fuse in pairs to produce myxamoebæ. Swarm cells frequently amoeboid and devoid of flagella. Myxamoebæ small, 15-30 μ diam. containing many nuclei. Spore tetrad arising from myxamoeba, each nucleus of which before reduction division being the nucleus of the tetrad" (Cook, 1933b).

Parasitic in stalks of *Ruppia rostellata*, *Zannichellia palustris*, *Z. polycarpa*, FINLAND, GERMANY, FRANCE, GREAT BRITAIN.

Ostenfeld and Petersen (1930) cite *Thecaphora Ruppiiæ* Setchell (1924) on *Ruppia maritima* var. *rostrata* in the United States as synonymous¹ with *Tetramyxa parasitica*. These papers were not considered by Cook.

¹ Examination of the type specimen of *Thecaphora* kindly sent by Professor Lee Bonar, of the University of California, confirms this synonymy.

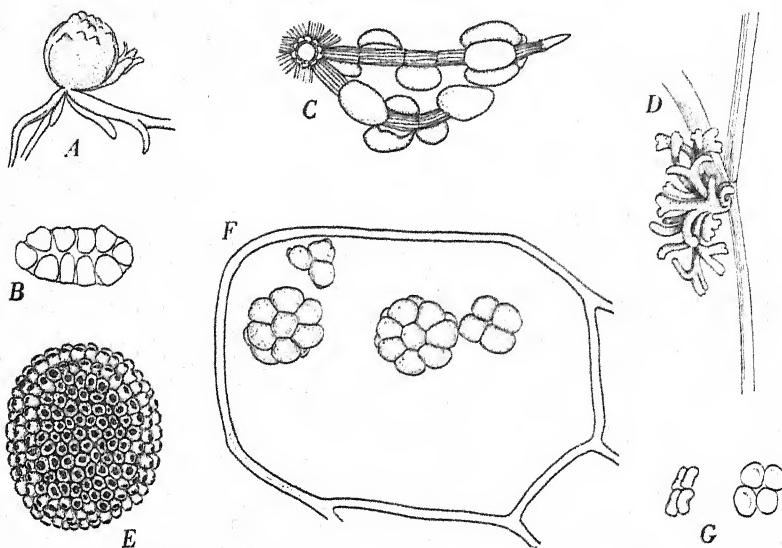


FIG. 45. Plasmodiophoraceae

A-B. Sorodiscus Callitrichis Lagerheim and Winge: *A*, gall on stem of *Callitrichia autumnalis* (enlarged); *B*, side view of cluster of spores. *C. Sorodiscus Karlingii* Cook on *Chara*, two of a whorl of leaves, showing strongly hypertrophied corticating cells on each leaf. *D. Sorodiscus Heterantherae* Wernham on *Heteranthera dubia*, group of hypertrophied adventitious roots, blackish gray with chalk-white tips (natural size). *E. Sporangia sorus of Sorodiscus Karlingii* Cook, composed of approximately two hundred cells. *F. Hypertrophied root cell of Heteranthera dubia* ($\times 750$) containing four groups of sori of *Sorodiscus Heterantherae* Wernham. *G. Tetramyxa parasitica* Goebel in *Ruppia* (?), two groups of four spores each, one in profile, one in face view.

(*A-B, G*, Winge, 1913; *C, E*, after Karling, 1928c)

SORODISCUS LAGERHEIM AND WINGE

Arch. f. Botanik, 12 (9): 23. 1913

(Figure 45 A-F)

"Spores arranged in flat spore-cakes two spores thick, without any hollow space between them. Individual spores urn-shaped, with an apical ring or collar. Spore cake enclosed in a common membrane which disorganizes when the spores are shed. One spore cake is the

product of a single myxamoeba. Spores on germination giving rise to swarm cells which develop into myxamoebae, fusion of swarm cells has not been seen. Meiosis occurring before spore formation. The organisms cause hypertrophy of the host tissue" (Cook, 1933b).

In aquatic angiosperms and Characeae.

Wernham (1935), in connection with a study of *Sorodiscus Heterantherae*, points out that Cook failed to consider the genus *Membranosorus*, established by Ostenfeld and Petersen (1930) on the basis of a fungus (*M. Heterantherae*) found by them on *Heteranthera dubia* in Canada. The resting spores formed a single layer, which lined the inner surface of the wall of infected cells. It seems possible from published accounts of the two fungi and from observations on a similar parasite of *Heteranthera* occurring in the vicinity of Ann Arbor, Michigan, that only a single species is involved. The question of the generic concept of *Sorodiscus* is another of the numerous problems in this group of fungi which await the results of new investigations.

KEY TO THE SPECIES OF SORODISCUS

On aquatic angiosperms

- On *Callitriche*; hypertrophied part globular *S. Callitrichis*, p. 507
- On *Heteranthera dubia*; hypertrophied part with finger-like out-growths *S. Heterantherae*, p. 508
- On *Chara* *S. Karlingii*, p. 508

SORODISCUS CALLITRICHIS Lagerheim and Winge

Arch. f. Botanik, 12 (9):23, pl. 1, figs. 9-10, pl. 2, pl. 3, figs. 43-64. 1913
(Figure 45 A-B)

"Spore-cakes composed of two layers of spores closely appressed to one another, 30-40 μ in diameter, containing up to 200 spores. Spores urn-shaped, or hexagonal, 6-7 μ long by 4-5 μ diam. Spores producing amoebae which grow into myxamoebae. Myxamoebae up to 60-40 μ each producing one spore-cake, and containing many nuclei. Reduction division occurring prior to spore formation" (Cook, 1933b).

Producing rounded galls 3-5 mm. in diameter on the host stem. Parasitic in *Callitriche stagnalis*, *C. vernalis*, NORWAY; *Callitriche autumnalis*, SWEDEN, RUSSIA.

SORODISCUS HETERANTHERAE Wernham

Mycologia, 27:272, figs. 1-18. 1935
(Figure 45 D, F, p. 506)

"Mature thallus a multinucleate flattened naked protoplast, various in shape and size, sometimes ellipsoidal and as little as 8 μ in diameter, but more typically a disc or ribbon which not infrequently encircles the host protoplast as a definite band which may reach 70 μ in length; vegetative mitoses cruciform; meiosis occurring in the mature thallus immediately preceding cytoplasmic cleavage and spore delimitation; a soral membrane not formed; spore aggregations extremely various in size, shape, and with respect to the arrangement of the spores in layers, but total number of spores in the aggregation believed to be always some multiple of four; single-layered sori common; sori with two complete layers exceptional; intermediate types abundant; some sori failing to show differentiation into layers; others definitely ribbon-like or plate-like and often tending to line the inner surface of the host wall more or less completely; individual spores at maturity globose to ovoid, 3.5-4.5 μ in diameter, buffy-brown (Ridgeway), and thick-walled; spore wall smooth, not always of uniform thickness, lacking an apical ring, collar or operculum, varying in thickness from 0.6 to 1.0 μ ; method of spore germination unknown; swarmspores not observed, and phase of life cycle outside of host not studied.

"Parasitic in *Heteranthera dubia* (Jacq.) MacM., causing formation of prominent dark olive brown to black galls, 0.5-3.0 cm. in diameter, on the true and adventitious roots; galls characterized by finger-like projections, 0.5-1.5 cm. in length, and containing the organism within their cells [United States]" (Wernham, *loc. cit.*).

See the remarks under the genus (p. 507).

SORODISCUS KARLINGII Cook

Arch. Protistenk., 80:207. 1933
(Figure 45 C, E, p. 506)

"Spore cake composed of two layers of closely appressed spores, 15 μ wide and 70 μ in length, containing upwards of 100 spores. Spores spherical, angular in outline, with their apical ends produced into caps. Myxamoebae becoming multinucleated, up to 90 μ diam." (Cook, *loc. cit.*).

Causing pronounced swelling of the infected parts. Parasitic in internodal cells of *Chara contraria* and *C. delicatula*, UNITED STATES.

The species is based on an unnamed form described by Karling (1928c).

IMPERFECTLY KNOWN GENUS OF THE PLASMODIOPHORACEAE

? PYRRHOSORUS JUEL

Bih. Kgl. Svensk. Vetensk.-Ak. Handl., 26, Afd. 3, No. 14:12. 1901

? PYRRHOSORUS MARINUS Juel

Op. cit., p. 12, pl. 1

Thallus at first plasmodial, later fragmenting into free ellipsoidal or fusiform naked uninucleate cells; sori from larger rounded mother cells, about 8μ in diameter, which occur with the sterile fusiform cells; sporangia naked, with orange granules, divided by three successive divisions into a naked mass of eight rounded cells, which become the zoospores; zoospores about 4.5μ long by 2.5μ wide, pyriform with an orange pigment spot and two lateral oppositely directed flagella.

Saprophytic in *Cystoclonium purpurascens*, in aggregate causing bright orange spots, SWEDEN.

There are a number of puzzling features about this fungus. From the description it is difficult to understand the relationship of the plasmodial thallus, which fragments into the spindle-shaped cells, to the sori of sporangia. There is a possibility that two organisms are involved, a *Labyrinthula*—often found, as was *Pyrrhosorus*, in decaying algae in marine aquaria—and a *Woronina*-like fungus to which the sori and zoospores belong. Winge (1913), who points out the resemblance of *Pyrrhosorus* to *Sorolpidium*, a parasite of beets, gives the following account of the life history: Infection is presumably caused by the zoospore, which penetrates the alga. Inside the host several myxamoebae are found, some small with a single large nucleus, others larger with many small nuclei. Juel thinks it possible that the large multinucleate thalli have arisen either by divisions of the single nucleus of the smaller thalli or by the fusion of uninucleate plasmodia. The single large nucleus of the smaller thallus, he believes, has simply

enlarged after establishment in the alga. The multinucleate plasmodium may be extensive and penetrate a great number of cells. Eventually it becomes walled and within it are formed either a close aggregation of numerous small uninucleated spindle-shaped cells, which round off and become the "spore mother cells," or scattered spindle-shaped cells, which sometimes also eventually become spore mother cells. The closely aggregated, uninucleated, naked spore mother cells may frequently have intermixed with them sterile cells which degenerate. Each of the spore mother cells and its nucleus undergoes three successive divisions. In this manner the cell becomes divided into eight biflagellate zoospores, each with two lateral flagella.

SAPROLEGNIALES¹

THE order Saprolegniales includes what are probably the best and most widely known species of aquatic Phycomycetes. Its members have long been the object of extensive morphological, physiological, and taxonomic studies. Indeed, the terms "water mold" and "fish mold" as ordinarily used refer only to members of one family, the Saprolegniaceae. Most of the species belonging to the order are saprophytic on plant and animal debris lying in fresh water. A few are parasitic on fresh-water and marine algae, especially diatoms, and on the roots of terrestrial flowering plants. *Sommerstorffia spinosa* is a predaceous parasite of microscopic animals, particularly rotifers. Tiffany (1939a, 1939b) has recently reviewed the relationship of species of *Saprolegnia* to diseases of fish and amphibia and has added new experimental evidence on the parasitism of these fungi. Nearly all the members of the largest family, the Saprolegniaceae, may be grown in pure culture on artificial media.

Although the designation "water mold" would seem to indicate that the Saprolegniaceae occur exclusively in water, recent investigations have shown otherwise. Numerous species have been isolated from the soil and some are thus far known only from that habitat. This naturally leads to the speculation whether they are not primarily soil organisms and merely adventitious inhabitants of the water. The general structure of the thallus and the fact that the free-swimming zoospore is ordinarily the nonsexual propagative unit seem, however, to argue for their being primarily aquatic.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

The thallus of members of the Saprolegniaceae is a richly branched coenocytic aggregation of hyphae, usually with unlimited capacity for growth. This aggregation may be pustular or form dense turf;

¹ As was mentioned in the Preface, the Saprolegniaceae, the largest family of this order, are not treated in the present volume. It would seem desirable, however, to include a brief consideration of the principal features common to all the Saprolegniales. For a more detailed account of the Saprolegniaceae see the monographs of Humphrey (1893), Minden (1915), Coker (1923), Coker and Matthews (1927), and the general discussion by Fitzpatrick (1930).

it is easily visible macroscopically on the substratum. In the Ectrogellaceae and Thraustochytriaceae, however, the body is of very simple structure, of limited growth, saccate, and distinctly chytrid-like.

Characteristically, the thallus walls in all members of the order give a pronounced cellulose reaction with chloriodide of zinc. In the hypha-forming species there does not appear to be, as in the Leptomitales, a strong differentiation of the lower part of the thallus into a basal cell and a holdfast system. The multinucleate contents are not highly refractive except in actively growing regions. Frequently they are somewhat thin and watery in appearance, with the granules arranged in a loose longitudinally disposed reticulum around the periphery of a central vacuole. Cross walls are laid down in normal material of eucarpic species only to delimit the reproductive organs and "gemmae" (chlamydospores). The latter are simply distended parts of the hyphae, of somewhat variable shape and often formed in catenulate series, within which the protoplasm accumulates. They may eventually disarticulate and, upon the advent of favorable conditions, germinate to produce either hyphae or short-stalked zoosporangia.

REPRODUCTION

Nonsexual Reproduction

Nonsexual reproduction is ordinarily accomplished by means of zoospores borne in zoosporangia. The zoospores, after escape, swarm, but eventually come to rest and germinate to form a new mycelium. The uninucleate swarmers are cleaved out within the sporangium and discharged after a highly characteristic and distinctive series of cytoplasmic changes (see Büsgen, 1882; Hartog, 1886-87; Rothert, 1888; Humphrey, 1893; Schwartz, 1922; Couch, 1924). Briefly, these changes as noted by Hartog and, particularly, by Humphrey are as follows:

1. The protoplasm in the young sporangium at first surrounds a central axial vacuole.
2. Irregular lines of cleavage extend outward from the central vacuole. These increase in number, connect with one another, and delimit the spore initials as irregularly polygonal uninucleate masses. At this time, if at all, the discharge papilla makes its appearance.
3. A homogeneous stage develops abruptly, accompanied by a

loss of turgidity of the sporangium. The cleavage lines or extensions of the central vacuole now suddenly become invisible because of the increase in size of the zoospore initials. Small vacuoles appear and disappear in these initials, the contents of which become less granular. Fluid, possibly of vacuolar origin, is probably expelled at this time.

4. The small vacuoles vanish, the cytoplasm again becomes granular, and the zoospore initials contract and separate into rounded individuals.

The later behavior of the zoospores differs according to the genus involved. In the Saprolegniaceae, the method of zoospore liberation and the subsequent behavior of the escaped zoospores are relatively constant in a given fungus and of great diagnostic importance in distinguishing genera. Diplanetism is present in *Isoachlya*, *Saprolegnia*, *Leptolegnia*, and in certain species of *Ectrogella*. Vestiges of it, according to most interpretations, are to be found in all members of the order. Monoplanetism occurs only in the genus *Pythiopsis*, in which the emerging zoospores are of the primary type described below. After encystment they germinate directly to form a mycelium. Diplanetism, as here understood, refers to the successive formation by a single fungus of *two different types of zoospores*. The primary zoospore is pyriform or "pip-shaped," with two apical flagella. It encysts after a period of swarming and gives rise to a "secondary" zoospore, which is reniform or grape-seed-like and bears two laterally attached oppositely directed flagella. Further encystments of the secondary zoospore have been observed (Weston, 1919; Salvin, 1940; etc.), but when they occur, the succeeding swarmer is always of the secondary type. The number of such "repeated emergences" (Weston, *loc. cit.*) is, as Salvin has emphasized, no doubt often influenced by the environmental conditions (lack of food, cool temperature, aeration) prevailing in the medium. Coker and Matthews (1937) apply the term "monocystic" to zoospores which encyst once before germinating, and "dicystic" to those which encyst twice.

Sexual Reproduction

Sexual reproduction is accomplished in most genera by the formation of oögonia and antheridia. One or several eggs (oöspheres), devoid of periplasm, are formed from the contents of the oögonium. This structure, as well as the eggs, is at first multinucleate. At maturity, however, only a single nucleus is present in each egg. The

antheridial branches, at the tip of which the antheridia develop, may arise from the same or different thalli. If only antheridia are formed by one thallus and oögonia by another (*Dictyuchus monosporus* [J. N. Couch, 1926b], *Achlya bisexualis* [Coker and A. B. Couch, in Coker, 1927]) the species is considered heterothallic. If both types of sex organs are produced on a single thallus it is homothallic. In some instances antheridia occur only on a small percentage of oögonia or are completely lacking. When they are not formed the eggs mature parthenogenetically (apogamously). Monandrous or polyanandrous conditions occur. In some species well-developed fertilization tubes are formed by the antheridia. Whether or not fertilization always takes place if antheridia are present has been a matter of considerable discussion in the past (Coker, 1923; Fitzpatrick, 1930). The male gamete is never flagellate and, like the female, never makes contact with the outside medium.¹

The mature oöspore is surrounded by a thick wall. The contents consist of a finely granular matrix within which are formed, typically, numerous small fatty droplets which surround wholly or in part a single large globule or several smaller ones. The structure of the egg in the Saprolegniaceae is of considerable taxonomic importance. According to Coker (1923:10), it falls into two main types:

... In all cases the fatty reserve is on or near the periphery, but in one type it is in the form of small droplets entirely surrounding the protoplasm, while in the other it is collected into one or a few larger drops on one side. The first of these types is called centric, the second eccentric, but intergrading types occur which connect the two extremes, and for certain of these I have found it useful to introduce the word subcentric. The three terms may be defined as follows:

A *centric* egg has one or two layers of small fat droplets entirely surrounding the central protoplasm.

A *subcentric* egg has the protoplasm surrounded by one layer of droplets on one side and two or three layers on the other, or rarely with the droplets entirely lacking on part of one side as in *Achlya oblongata*; this last condition connecting directly with such eccentric structure as is shown by *Pythiopsis cymosa*.

¹ Apinis (1935) has described as *Archilegnia lativica* a saprolegniaceous fungus in which the eggs are said to be fertilized by minute uniflagellate free-swimming male gametes. As has been pointed out by Coker and Matthews (1937), recognition of such an aberrant organism must be withheld until a further study is made. From the figures given, it is entirely possible that the material carried a persistent monad infection.

An eccentric egg has one large drop on one side either outside the protoplasmic surface or barely enclosed by a thin layer of protoplasm, or several large drops enclosed in the protoplasm on one side, or a lunate row of small drops (in optical sections) on one side, as in *Pythiopsis cymosa*.

After a period of rest the oöspore germinates to produce a tube which either elongates and reëstablishes the thallus or forms a sporangium at its tip. The plant body presumably is always haploid, the only diploid structure being the oöspore.

Couch (1926b) has established heterothallism or, better, dioecism in the ubiquitous water mold *Dictyuchus monosporus*. When the oögonial and the antheridial plants bearing sexual organs were isolated and grown separately oöspore formation did not occur. When, however, the two strains were grown together sex organs were formed and mature oöspores were produced wherever the hyphae of the two intermingled. Contact of the two strains was necessary and seemed to be the only type of stimulation concerned in the process. Environmental conditions had only a secondary and variable effect. Intercrosses between the four recognized species of the genus were successful, and the resulting variations in morphological characters, hitherto supposed to be of specific significance, were so marked as to invalidate all but the type species, *D. monosporus*. Male, female, and neutral strains were found to occur in nature, as well as one which formed its oöspores parthenogenetically. Oöspores of this last strain were germinated and the mycelium thus produced was crossed (1) with a male strain, which was, as a consequence, stimulated to the formation of (functional?) antheridia that applied themselves to the oögonia produced by the parthenogenetic strain; (2) with an oögonial strain, in which experiment oögonia were formed on both strains and, in addition, functional antheridia were also produced on the parthenogenetic strain. Thus the latter strain was shown to be inherently monoecious. Germination of the oöspores formed by dioecious strains disclosed an interesting fact, namely, that parts of the mycelium arising from the germ hypha were male, parts female, and parts mixed. This seems to indicate that sexual segregation took place early in the process of germination. If the germ hypha gave rise to a sporangium, the segregation probably occurred in the cleaving-out of the zoospores, since some of the latter gave rise to male, some to female, and some to mixed mycelia.

Homothallism or monoecism has been definitely proved in *Leptolegnia* (Schlösser, 1929) and in certain species of *Saprolegnia*, *Achlya*,

and *Protoachlyja* (Schlösser, *loc. cit.*). Schrösser (*loc. cit.*) has also given some interesting details of regeneration and "reversal" in the isolated diclinous sex organs of certain homothallic species. At all stages in their development before actual fertilization the antheridia and the oögonia can, by alterations in the environment, be made to reverse the sequence of their protoplasmic changes and hence to become again vegetative in character. Further, if sex organs are placed under conditions favorable for sporangial formation they may, if the process of fertilization has not been initiated, be converted into sporangia and produce functional zoospores. It has also been found in certain groups of *Saprolegnia*, in which species are differentiated mainly on the number of oögonia supplied with antheridia, that this character can be modified considerably in a single form by changing the temperature at which growth takes place. A number of other valuable observations are made in Schrösser's excellent paper.

Recent highly interesting investigations by John Raper (1939a, 1939b, 1940) have revealed conclusively that in at least one heterothallic member of the order, *Achlya ambisexualis*, hormones play a part "in initiating and coordinating the several stages of the sexual process . . ." The chief results of Raper's study may be summarized as follows:

The formation by the fungus of three hormones, A, B, and C, was postulated and the sequence of their activity confirmed by experimental methods. Hormone A is formed by the female plant and acts to initiate the production of antheridial hyphae by the male plant before contact is established with the female mycelium. This hormone is produced at all times, regardless of the age of the plant. Hormone B is formed by the antheridial (not the vegetative) hyphae and initiates the development of oögonial initials on the female hyphae. Hormone C is formed by the oögonial initials and serves to attract the antheridial hyphae to their vicinity and also to delimit the male gametangium. Raper continues:

In matings of male and female strains on a favorable agar medium sexual activation of the male plant frequently occurs when the two mycelia are 3–5 mm. apart; activation of the female mycelia often occurs before contact of the two thalli. Following the time of intermingling of the hyphae of the two mycelia, production of antheridial branches and oogonial initials spreads over the entire male and female mycelia respectively.

In water matings of male and female plants, in addition to the functional sexual organs along the line of intermingling, antheridial branches are pro-

duced around the circumference of the male mycelium, and oogonial initials are formed scattered over the entire female mycelium.

Both male and female plants are sexually activated when grown or placed on opposite sides of a cellophane membrane. The different stages of the sexual reaction occur in their natural sequence until the time of oogonial delimitation.

Male plants produce antheridial hyphae when placed in water in which a female has previously grown. A female produces oogonial initials when placed in water in which a male has produced antheridial hyphae, though it is not activated in water in which a vegetative male has grown.

PHYSIOLOGICAL INVESTIGATIONS

The classic physiological investigations of Klebs (1896, 1898, 1899, 1900) on *Saprolegnia*, which were followed by those of Kauffman (1908), Obel (1910), Pieters (1915), and others, have furthered enormously our knowledge of the underlying factors determining the growth and reproduction of members of the Saprolegniales and of aquatic Phycomycetes in general. The conditions necessary to growth have been summarized by Coker from Klebs as follows (see Coker, 1923):

1. Uninterrupted continuous growth:—in all good nutrient media, so long as fresh unaltered nutrient is present, e.g., in water with peas, in weak meat extract (1-2%), in gelatin with peptone, in mixtures of water with albumen, casein, etc.
2. Prompt and complete transformation of the mycelium into sporangia and zoospores:—by placing a well-nourished mycelium in fresh water.
3. Growth with continuous formation of zoospores:—in very weak solution of certain nutrients, e.g. 0.005% haemoglobin, also in mycelium on agar-albumen jelly that is put in running water.
4. Active formation of oogonia with limited growth:—by putting a well-nourished mycelium in agar-agar.
5. Active growth, then active formation of oogonia:—
 - (a) oogonia with antheridia:—in solution of leucin (0.1%) with tricalcium phosphate (0.1%).
 - (b) oogonia without antheridia:—in solution of haemoglobin (0.05-0.1%).
6. Growth, then formation of sporangia, then of oogonia:—by placing the mycelium in water from gelatin-meat extract; or by culture on dead insect in water.
7. Growth and simultaneous formation of sporangia and oogonia:—in water with some fibrin or syntoinin.

8. Growth, then formation of oogonia and later sporangia:—after strong nutrition of the mycelium transfer to 0.01% haemoglobin.

9. Active formation of gemmae:—by putting a well-nourished mycelium in 0.6% tricalcium phosphate, or 1% sodium chloride, etc.

10. Growth with sporangia, then gemmae; or growth with oogonia, then gemmae; or growth with sporangia and oogonia and then gemmae:—in the items 3, 5 and 6 above, when the culture is continued to the complete exhaustion of the nutrient material.

General conclusions in regard to conditions for the formation of sex organs are summarized as follows (Coker, *loc. cit.*, p. 44):

1. In a mycelium which is constantly given fresh nourishment no oogonia are ever formed. Young, just formed oogonia were, by means of fresh, soluble food, induced to vegetative growth. The old were, however, killed.

2. If a strongly nourished mycelium is changed to a medium of low nutritive value (in which the formation of sporangia is rare or absent) oogonia are formed in a few days.

3. In a good soluble food, preferably at such concentration that the sporangia cannot be formed, the mycelium begins to form oogonia as soon as the solution is chemically changed on account of its growth, and has lost its nutritive value.

4. The formation of oogonia is particularly encouraged through phosphate, which is likewise necessary to the formation of the antheridia. In a soluble food that is poor in phosphate oogonia are formed, but no antheridia; particularly abundant are such oogonia in a pure solution of haemoglobin.

5. In many soluble foods, for example in peptone, gelatine, etc. are excreted certain products of assimilation of the mycelium which hinder the formation of oogonia.

SYSTEMATIC ACCOUNT

SAPROLEGNIALES

MICROSCOPIC, saprophytic or parasitic, aquatic or terricolous fungi; the thallus endobiotic or more commonly partly within and partly outside the substratum; holocarpic or eucarpic; when eucarpic the hyphae without constrictions and of unlimited growth; septa formed only in eucarpic species, where they delimit reproductive organs; walls turning blue with chloriodide of zinc; contents granular, refractive only in growing tips; gemmae present or absent; zoospores formed

in sporangia, which in certain genera may be internally proliferous; zoospores biflagellate or (in *Geolegnia*) lacking flagella, mono- or diplanetic, if diplanetic the primary zoospore somewhat pyriform or pip-shaped, with two anterior flagella, the secondary zoospore reniform or grape-seed-like with two lateral or subapical oppositely directed flagella, capable in some individuals of repeated encystments and emergences before germination; sexual reproduction oögamous, plants homo- or heterothallic, gametes never flagellate nor set free in the medium; oögonium producing one or more eggs without periplasm; antheridium (occasionally nonfunctional or lacking) usually forming a fertilization tube; oöspore thick-walled, characteristically with a large reserve globule (partly or completely surrounded by one or more layers of minute globules) and a lateral bright spot, upon germination forming a mycelium or a short hypha terminated by a zoosporangium.

The order as here defined excludes the Leptomitaceae of older authors, which has been raised by Kanouse (1927) to ordinal rank.

The Saprolegniales consists of three families, the Ectrogellaceae, Thraustochytriaceae, and Saprolegniaceae. The Ectrogellaceae include simple endobiotic holocarpic fungi which strongly resemble endobiotic true chytrids in their body characteristics. The Thraustochytriaceae, based on a eucarpic marine form, *T. proliferum*, saprophytic on *Bryopsis*, approximate in their bodily organization a species of the chytridiaceous genus *Rhizophyridium*, the sporangium being epibiotic and the vegetative system within the alga rhizoidal. The members of both these families, however, show unmistakable affinities with the Saprolegniaceae. In the Ectrogellaceae features such as the sequence of changes in the maturing sporangium, the diplanetic character of the biflagellate zoospores, and the cellulose wall are all saprolegniaceous. Although the affinities of *Thraustochytrium* are as yet somewhat obscure, its *Thraustotheca*-like method of zoospore discharge, the biflagellate zoospores, and internal proliferation of the zoosporangium all point to a relationship with the Saprolegniaceae.

KEY TO THE FAMILIES OF THE SAPROLEGNIALES

Thallus holocarpic, endobiotic during development, more or less extramatrical at maturity; zoospores mono- or diplanetic, behaving variously after discharge; primarily parasites of freshwater and marine diatoms and Phaeophyceae ECTROGELLACEAE, p. 520

Thallus eucarpic, intra- and extramatrical; saprophytic or parasitic on a wide variety of substrata

Thallus resembling that of a monocentric chytrid, the reproductive rudiment epibiotic, the vegetative system rhizoidal

THRAUSTOCHYTRIACEAE, p. 538

Thallus consisting of a more or less well developed complex of tubular hyphae without constrictions, the extramatrical parts of which bear numerous reproductive organs

SAPROLEGNIACEAE, p. 540¹

ECTROGELLACEAE

Thallus endobiotic, sometimes more or less extramatrical at maturity, one-celled, unbranched or sparingly branched, holocarpic, walls turning blue with chloriodide of zinc, contents at first vacuolate, later coarsely granular; sporangium inoperculate with one or more discharge pores which are sessile or at the tips of tubes; zoospores segmented within the sporangium, diplanetic, primary zoospores biflagellate, after discharge either undergoing a short period of motility before encysting or encysting at once, secondary zoospores laterally biflagellate; resting spore thick-walled, filling or lying loosely in a thin-walled containing structure, contents with globules, germination not observed, antheridial cell reported in one species.

Endobiotic holocarpic saprolegniaceous parasites of fresh-water and marine Bacillarieae, of marine Phaeophyceae, and of Rhodophyceae.

KEY TO THE GENERA OF THE ECTROGELLACEAE

Sporangium unbranched

Parasitic in diatoms; zoospores generally encysting outside the sporangium; cysts spherical ECTROGELLA, p. 521

Parasitic in the Phaeophyceae and Rhodophyceae; zoospores encysting within the sporangium or outside; cysts angular

Sporangium becoming partly extramatrical at maturity; zoospores encysting within the sporangium ("net-sporangium") or emerging at once EURYCHASMA, p. 527

¹ Only a diagnosis of the family and Coker and Matthews' key to the genera are included in this text.

- Sporangium remaining endobiotic at maturity; zoospores encysting outside EURYCHASMIDIUM, p. 532
 Sporangium branched APHANOMYCOPSIS, p. 535

ECTROGELLA ZOPF

Nova Acta Acad. Leop.-Carol., 47:175. 1884. Emend. Scherffel, Arch. Protistenk., 52:5. 1925
 (Figure 46 A-C, G-J, p. 524)

Thallus endobiotic, tending to force apart the valves of the host and to become partly extramatrical, holocarpic, without a specialized vegetative system, tubular or occasionally rounded, unbranched, contents at first vacuolate, later coarsely granular; sporangium bearing from one to many short conical discharge tubes; zoospores formed in the sporangium, diplanetic, primary spores biflagellate or nonflagellate, swimming directly away or encysting at the orifice, secondary spores, where known, biflagellate; resting spore endobiotic, thick-walled, completely filling or lying loosely in a saclike containing structure, accompanied (in one species) by a companion cell, germination not observed.

Parasites of fresh-water and marine diatoms.

A relatively poorly known group of minute parasites. Zopf stated that the zoospores were posteriorly uniflagellate, but Scherffel has shown them to be biflagellate and diplanetic. The genus as understood here is confined to parasites of diatoms. Scherffel (*loc. cit.*), however, has suggested the inclusion of the phaeophycean parasite *Eurychasma* in *Ectrogella*.

The discharge tubes of *Ectrogella*, rather than boring through the siliceous wall, gain access to the outside of the diatom by expansion of the thallus, which forces apart the valves of the host.

KEY TO THE SPECIES OF ECTROGELLA

Sporangium narrowly tubular, with or without an equatorial swelling, discharge tubes short

Sporangium predominantly narrowly tubular throughout, discharge tubes numerous; primary zoospores flagellated and undergoing a short period of motility before encysting

E. Bacillariacearum, p. 522

Sporangium predominantly tubular with an equatorial swelling, discharge tube single; primary zoospores nonflagellate, encysting at the orifice after discharge *E. monostoma*, p. 523

- Sporangium predominantly broadly cylindric-oblong, or ovoid, or lenticular or spherical, discharge tubes of variable length
- Sporangium broadly cylindric-oblong, or ovoid; primary zoospores nonflagellate, encysting at the orifice after discharge
- Sporangium predominantly broadly cylindric-oblong, discharge tubes short, generally two, placed near one end of the sporangium *E. Gomphonematis*, p. 523
- Sporangium predominantly ovoid, discharge tubes slightly prolonged, from two to ten, often opposite, formed at any place on the sporangium *E. Licmophorae*, p. 525
- Sporangium predominantly spherical or lenticular; primary zoospores flagellate, swimming directly away after escape
- E. perforans*, p. 526

ECTROGELLA BACILLARIACEARUM Zopf

Nova Acta Acad. Leop.-Carol., 47:175, pl. 16, figs. 1-24. 1884. Emend. Scherffel, Arch. Protistenk., 52:5, pl. 1, figs. 1-9. 1925
 (Figure 46 A, p. 524)

Sporangium tubular, fusiform, ellipsoidal or occasionally spherical, variable in size, up to 200 μ or more in length, unbranched, generally forcing apart the valves of the host, wall thin, smooth, colorless, discharge tubes short, thick-walled, from one to ten, arranged in one or two files corresponding in position to the girdle bands of the host cell; primary zoospores moving within the sporangium, pyriform, 4 μ long by 2 μ wide, with two equal, laterally inserted flagella 4 μ long, cysts spherical, not grouped compactly at the orifice, secondary zoospores ovoid, with an anterior broad oblique cleft, flagella unequal, movement darting, with pauses and frequent changes of direction; resting spore not observed.

Parasitic in *Synedra sp.*, *S. lunularis*, *Gomphonema sp.*, *Pinnularia sp.*, Zopf (*loc. cit.*), GERMANY; *Synedra ulna*, *Meridion circulare*, Scherffel (*loc. cit.*; 1902b), Domján (1936:52, pl. 1, fig. 167), HUNGARY; *Synedra sp.*, *Gomphonema sp.* (coll. de Wildeman, Marchal), de Wildeman (1890:26), BELGIUM; diatoms, de Wildeman (1894:155), FRANCE; diatoms, de Wildeman (1895a:65), SWITZERLAND; diatoms, Atkinson (1909a:338), *Pinnularia sp.*, Sparrow (1933c: 531), UNITED STATES.

The species has generally been found in the early spring. Zopf observed that in nature about 75 per cent of the diatoms were in-

fected, and under laboratory conditions nearly 100 per cent. He concluded that this was due to the enormous numbers of zoospores produced.

When more than one thallus is formed in the host cell (occasionally as many as thirty appear there), its tubular shape is lost and it tends to become more ellipsoidal or spherical. Aside from differences already noted in the zoospore, Scherffel observed that the primary swarmer does not contain the solitary globule characteristic of the chytrid spore, but, rather, bears posteriorly several refractive granules. The secondary spore, on the other hand, contains dense hyaline plasma anteriorly and one or more large refractive droplets posteriorly. In the behavior of the zoospores the species is said by Scherffel to resemble *Saprolegnia*, that is, the primary zoospores undergo a period of motility before encysting.

ECTROGELLA MONOSTOMA Scherffel

Arch. Protistenk., 52:8, pl. 1, figs. 10-19. 1925

Sporangium long, tubular, 4-8 μ wide, with a pronounced equatorial swelling, unbranched, wall extremely thin, colorless, smooth, discharge tube single, short, 2-3 μ in diameter, formed on the swelling; primary zoospores few, not swarming in the sporangium, without flagella, after escape encysting in a group at the orifice, cysts 6-8 μ in diameter, secondary zoospores grape-seed-like, with a ventral furrow, 8 μ long, with two lateral oppositely directed flagella; resting spore not observed.

Parasitic in *Synedra ulna*, Scherffel (*loc. cit.*), HUNGARY; *Pinnularia* sp., Sparrow (1933c:531), UNITED STATES; *Synedra* sp., Sparrow (1936a:461, fig. 4p), ENGLAND.

The valves of the host are forced apart by means of the equatorial swelling, and the discharge tube protrudes free in the medium.

ECTROGELLA GOMPHONEMATIS Scherffel

Arch. Protistenk., 52:9, pl. 1, figs. 20-21. 1925

Sporangium broadly cylindric-oblong, about 21 μ long by 6 μ wide (calculated), unbranched, forcing apart the valves of the host, wall thin, smooth, colorless, discharge tubes broad, short, thin-walled, lateral, generally two, placed near one end; primary zoospores from

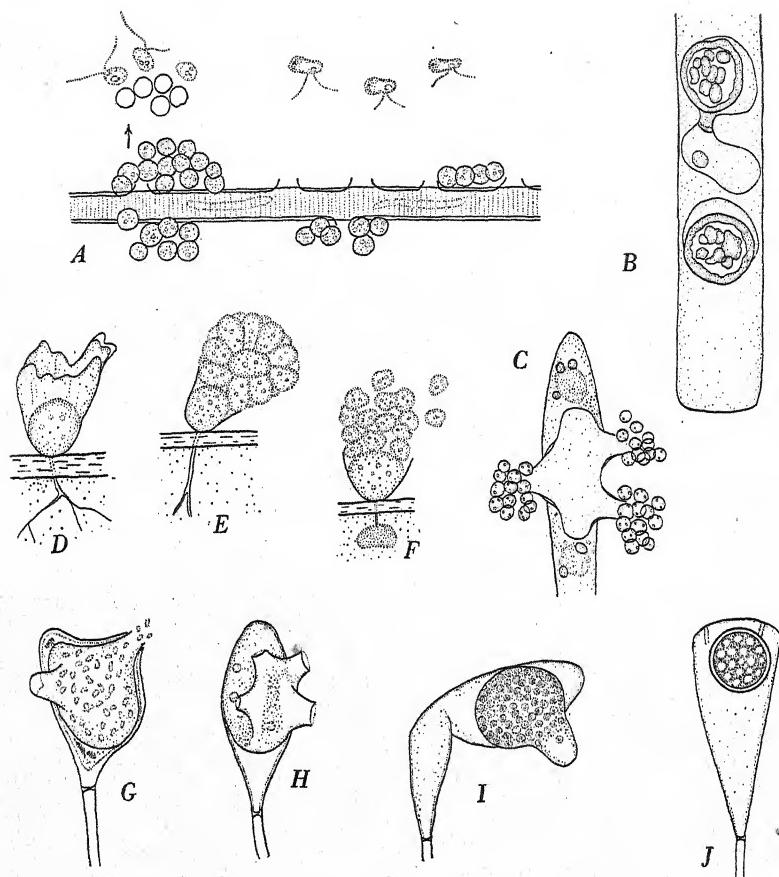


FIG. 46. Ectrogellaceae and Thraustochytriaceae

A. *Ectrogella Bacillariacearum* Zopf, portion of the diatom *Synedra*, within which part of a discharged sporangium is shown; outside the host, near orifice of discharge tubes of fungus, are groups of encysted primary zoospores; above arrow are secondary zoospores which have emerged from cysts, and above to the right are primary zoospores with rudimentary flagella.

B-C. *Ectrogella Licmophorae* Scherffel in *Licmophora*: **B**, two resting spores ($\times 540$), upper one apparently formed after a sexual process; supposed antheridial cell is empty save for single globule; **C**, discharged zoosporangium with groups of encysted primary zoospores at orifices of discharge tubes ($\times 600$); base of each of latter structures is thick-walled, forming a "forcing

fifteen to eighteen, swarming within the sporangium, ovoid, 3μ long, with a single refractive granule and two equal subapical posteriorly directed flagella longer than the body, encysting at the orifice in a group, cysts 3μ in diameter, with a large refractive globule, secondary zoospores not observed; resting spore not observed.

Parasitic in *Gomphonema micropus*, HUNGARY.

Differing from *Ectrorella Bacillariacearum* primarily in having an *Achlya*-like rather than a *Saprolegnia*-like type of spore discharge.

ECTROSELLA LICMOPHORAE Scherffel

Arch. Protistenk., 52:10, pl. 1, figs. 22-30. 1925

(Figure 46 B-C)

Sporangium predominantly ovoid and olpidioid, occasionally irregularly saccate, $7-25 \mu$ long by about 7μ in diameter (calculated), wall smooth, thin except at the base of the discharge tube, where it is thickened to form a "forcing apparatus," discharge tubes from two to ten (rarely one), slightly prolonged, broadly conical, often emerging from opposite sides and giving a starlike appearance; primary zoospores pyriform, 3μ long, with two apical posteriorly directed flagella, assuming motility within the sporangium, upon emergence encysting in a group at the orifice of the discharge tube, cysts 3.5μ in diameter, secondary zoospores not observed; oöspore (one instance) subspherical, 12μ in diameter, with a thick smooth colorless wall, contents with large irregular fat clods, not filling the oögonium, the latter spherical, thin-walled, 14μ in diameter, germination not observed; antheridium consisting of a single saclike

apparatus"; frustule of diatom abnormally swollen. *D-F. Thraustochytrium proliferum* Sparrow ($\times 760$) on *Bryopsis plumosa*: *D*, discharged primary sporangium with secondary sporangium beginning to enlarge within it; *E*, mature primary sporangium showing basal body which will become rudiment of secondary sporangium; *F*, liberation of spores after deliquescence of upper part of wall of primary sporangium; each of the spores later becomes biflagellate. *G-J. Ectrorella perforans* H. E. Petersen ($\times 430$) in *Licmophora*: *G*, abnormally swollen diatom with zoospores of fungus escaping through one of the two visible discharge tubes; *H*, empty sporangium with four visible discharge tubes; *I*, hypertrophied diatom with unopened sporangium within which is peripheral layer of quiescent zoospores; *J*, resting spore.

(*A-C*, Scherffel, 1925a; *D-E*, Sparrow, 1936b; *G-J*, Sparrow, 1934c)

structure almost equal in size to the oögonium, attached to the latter by a narrow tube.

Parasitic in *Licmophora sp.*, ITALY (the Adriatic, near Rovigno).

Although *Ectrogella Licmophorae* occurs in the same host as the following fungus, *E. perforans*, it differs from Petersen's species in several particulars, primarily in the encystment of the zoospores after discharge, the presence of the "forcing apparatus," the more irregular shape of the sporangium, and the fact that the oöspore lies loosely in the oögonium, to which the saccular antheridium is attached by a beaklike process (Fig. 46 B, p. 524).

ECTROGELLA PERFORANS H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):466, fig.

VII, 1-5

(Figure 46 G-J, p. 524)

Sporangium spherical, lenticular, or rarely irregularly saccate, 26-40 μ long by 20-35 μ in diameter, with a thin colorless wall, discharge tubes from one to five, broadly conical, 8-10 μ long by 9-12 μ in diameter; zoospores pyriform, 3 μ long by 2 μ wide, somewhat curved, with an anterior refractive droplet, the two flagella anteriorly (?) attached and oppositely directed, emerging individually through the large orifice of the discharge tube and swimming away immediately, movement an uneven rotation; resting spore spherical, 14-19 μ in diameter, with a smooth colorless double wall 2.5-3 μ thick, the outer wall thin, the inner thicker, contents with globules, germination not observed.

Parasitic in *Licmophora Lyngbyei* (abbreviata ?), *Synedra ulna* (?), Petersen (*loc. cit.*), *Licmophora sp.*, Sparrow (1934c:19, pl. 4, figs. T-Y), DENMARK; *Striatella unipunctata*, *Licmophora abbreviata*, Sparrow (1936b:239, pl. 3, fig. 2), UNITED STATES.

In most instances the discharge tubes gained access to the outside because the thallus of the fungus forced apart the valves of the host. It was noted (Sparrow, 1934c), however, that occasionally the diatom frustule was often considerably distorted, so much so as to suggest that the fungus had dissolved the siliceous material and produced hypertrophy of the cell (Fig. 46 G, I, p. 524). One un-

opened sporangium, presumably of this species, was found in which the mature zoospores were loosely disposed around the periphery of a large central vacuole (Fig. 46 I), exactly as in *Eurychasma*. No traces of a net sporangium could be detected. This observation lends some support to the contention of Scherffel (1925a) that *Eurychasma* should be merged with *Ectrogella*. In the Danish material a resting spore was found to which was attached a small hemispherical cyst, suggesting the occurrence here of an *Olpidiopsis*-like type of sexuality.

Stages in the penetration of the fungus into the diatom were observed in the American material. Many frustules bore quiescent zoospores on the outer surface. In several diatoms a needle-like penetration tube from the cystospore had pierced the cell wall. Actual passage of the fungous material was not, however, observed, although empty epibiotic cysts were found. Inside the cell the parasite assumed a central position, possibly attaching itself to the nucleus of the alga. Once established within the diatom it caused disarrangement of the chloroplasts and eventually their total destruction. At maturity the sporangium was surrounded by a few chestnut-brown residual granules, all that remained of the host contents.

Observations consistently showed that the fungus alone initiated the infection and, unaided by other biological agencies, brought about the complete disintegration of the diatom. During July infection of the diatoms assumed epidemic proportions, as many as eighty-eight per cent of a population being invaded by the fungus.

EURYCHASMA MAGNUS

Hedwigia, 44:347. 1905

(Figure 47, p. 530)

Thallus at first wholly endobiotic, at maturity bursting the distended host wall and becoming partly extramatrical, holocarpic, unbranched; sporangium with from one to several extramatrical discharge tubes, zoospores encysting within the sporangium or directly on emerging, laterally biflagellate; resting spore not observed.

So far as is known, this fungus occurs exclusively on marine algae.

See the remarks under *Ectrogella perforans*, above.

EURYCHASMA DICKSONII (Wright) Magnus

Hedwigia, 44:347. 1905

(Figure 47, p. 530)

Rhizophydiump Dicksonii Wright, Trans. R. Irish Acad. Dublin (Sci.), 26:374, pl. 6. 1879.

Olpidium Dicksonii (Wright) Wille, Vidensk. Selsk. Skr. Christiana (Mat.-Nat. Kl.), 1899, No. 3:2.

Ectrogella Dicksonii (Wright) Scherffel, Arch. Protistenk., 52:4. 1925.

Sporangium at maturity generally protruding from the host cell, extremely variable in shape and size, generally irregularly saccate, 25–80 μ high by 20–40 μ in diameter, with one or two broad short discharge tubes, wall thin, smooth, colorless; zoospores somewhat gibbose-pyriform, 5 μ long by 3 μ in diameter, with two unequal, subapically attached, oppositely directed flagella, emerging without encystment (?) or coming to rest and encysting within the sporangium ("net sporangium"), from which they eventually escape; resting spore not observed.

Parasitic in *Ectocarpus granulosus*, Wright (*loc. cit.*), IRELAND; *Ectocarpus confervoides*, *E. crinitus*, *E. pusillus*, Hauck (1878:321), ITALY; *Ectocarpus siliculosus*, Rattray (1887:589, pls. 147–148), SCOTLAND; *Ectocarpus Constanciae*, Hariot (1889:176), KERGUELEN; *Striaria attenuata*, Wille (*loc. cit.*), *Pylaiella littoralis*, Löwenthal (1905:225, pl. 7, figs. 3–7), NORWAY; *Punctaria* sp., *Stictyosiphon tortilis*, *Pylaiella littoralis*, *Ectocarpus* sp. (coll. K. Rosenvinge), Petersen (1905:476), GREENLAND; *Ectocarpus confervoides* (coll. Börgesen), Petersen (*loc. cit.*, p. 477), FAROE ISLANDS; *Ectocarpus* sp., *Stictyosiphon tortilis* (coll. K. Rosenvinge), *Akinetospora* sp., *E. confervoides*, *E. Sandrianus*, *Striaria attenuata*, *Stictyosiphon tortilis*, *Pylaiella littoralis*, Petersen (*loc. cit.*, p. 477, fig. VIII, 1–7), *Striaria attenuata*, Sparrow (1934c:5, pl. 1, figs. A–S), DENMARK; *Ectocarpus* sp., Pierre Dangeard (1934:69, pl. 8, figs. A–E), FRANCE.

This appears to be the most common and widespread of the marine fungi, although it has not as yet been reported from the Western Hemisphere. Considerable information has been collected with respect to its development and something is known of its cytology. Further study of the behavior of the zoospores is needed, however, particularly to ascertain whether or not they are diplanetic

when they swarm directly from the sporangium without previous encystment.

The zoospore upon coming to rest on the surface of *Striaria* encysts and produces a tenuous germ tube which penetrates the wall of the host and through which the protoplasm of the zoospore flows (Fig. 47 A, p. 530). After this discharge the empty cyst of the spore remains adherent, at least for a time, to the wall of the alga. Once infection is accomplished, the amoeboid-appearing plasma of the fungus increases in size and, though at first irregular in shape and scarcely distinguishable from the algal protoplasm, ultimately becomes a somewhat spherical refractive mass, which often occupies the center of the cell of the *Striaria* (Fig. 47 B-F). The latter is apparently stimulated to abnormal growth very early in the course of the infection.

The chloroplasts of the infected cell soon become discolored and disintegrate, and the residue of such material not utilized by the fungus may usually be observed as a peripheral brownish-green layer around the outside of the thallus. The wall of the host is eventually ruptured by the constantly enlarging fungus, which then protrudes into the outside medium (Fig. 47 K-M, p. 530). This liberation of the parasite from a wholly endobiotic existence is initiated by the formation on the thallus of one or, usually, two broad apical or subapical papillae which penetrate the algal wall (Fig. 47 G-J). Subsequent expansion and elongation of the parasite, if more than one papilla is formed, causes a part of the algal wall between the papillae to be carried up between the protuberances. The remainder of the wall persists around the more proximal portion of the sporangium.

The thallus is at first uninucleate, according to Löwenthal (*loc. cit.*). Petersen (*loc. cit.*) has described the sequence of changes which occur in the protoplasm of the developing thallus as follows:

1. Stage of ordinary protoplasm: Protoplasm dense with few vacuoles; nuclei in process of division.
2. Globular stage: Division of nuclei has been achieved as well as differentiation of zoospores. Little globular bodies closely packed in sporangium.
3. Foamy stage: Protoplasm with numerous large vacuoles. Zoospores invisible. Nuclei appear in large numbers in protoplasmic bridges between vacuoles. (Fig. 5 of Löwenthal.)

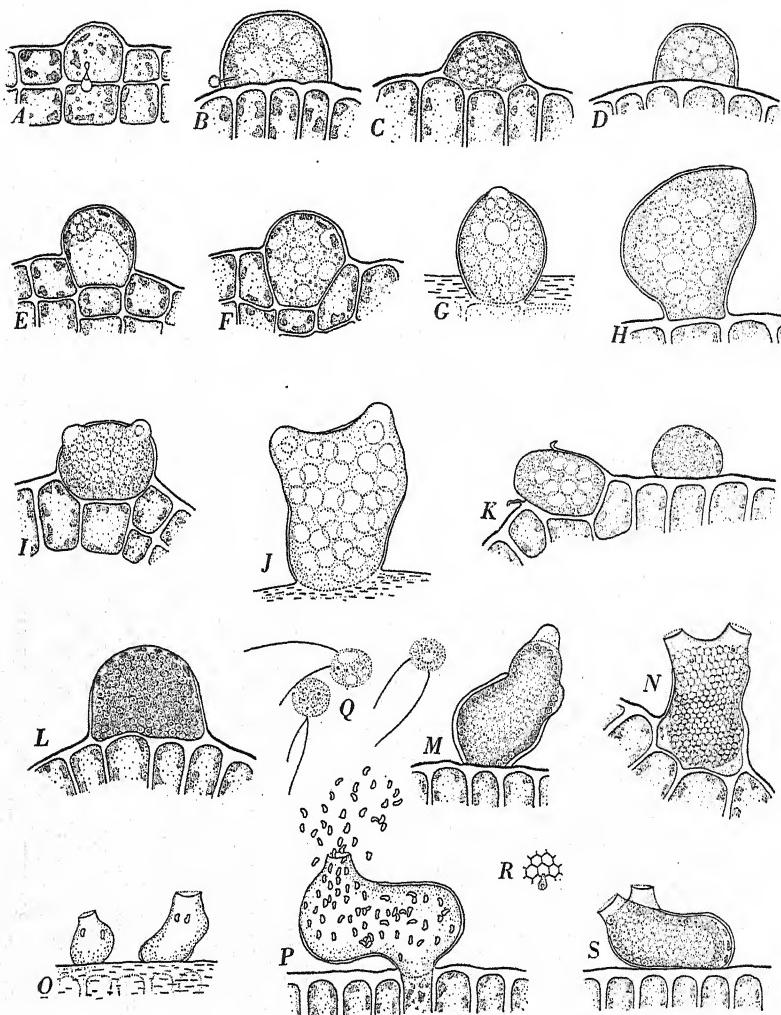


FIG. 47. Development of *Erychasma Dicksonii* (Wright) Magnus in *Striaria*

A. Zoospore infecting vegetative cell of *Striaria*; hypertrophy of host cell is evident. *B.* Empty cyst and infection tube of zoospore on hypertrophied host cell; thallus of fungus appears as irregular, somewhat refractive mass. *C-E.* Infected host cells showing spherical shape assumed by thallus of fungus; latter contains a number of highly refractive granules. *F.* Infected cell showing peripheral disposition of disintegrating chloroplasts. *G-I.*

4. Stage at which zoospores are regularly disposed against the wall. (Distinguishable from stage 2 only in the older condition of the sporangium and the more regular arrangement of zoospores against the wall.)

After the foamy stage there occurred a very strong contraction of the plasma, which lasted twenty minutes and during which protoplasmic threads united it to the host wall. Dilation then occurred and the foamy aspect disappeared. Differentiation of the zoospores took place during the period of dilation. When this was half over a certain number of zoospores had already assumed motility, and when dilation was at maximum all the zoospores were in motion. After a period of swarming, the zoospores again became immobile and encysted, forming a layer against the wall. Presumably they eventually escaped from their cysts and emerged through the open discharge tube, leaving behind a reticulum (net sporangium) of cyst walls. As has been previously indicated, it is not certain that encystment of the zoospores within the sporangium necessarily precedes emergence. In both open and unopened sporangia the mature zoospores are found forming a peripheral layer around a large central vacuole (Fig. 47 M, S). Possibly under favorable conditions the zoospores may emerge at once upon the deliquescence of the papilla (Fig. 47 O-Q), whereas if external conditions are unfavorable they encyst and only escape after the return of suitable environmental circumstances (Fig. 47 R). The earlier observations of Rattray

Formation of papillae by fungus during vacuolate stage. *J.* Extrusion of fungus from host cell by bursting of confining wall of latter; more distal portion of host wall may be seen between the two papillae. *K.* Two infected host cells; fungus to the left has burst host wall. *L.* Sporangium in which zoospores have been formed before extrusion from host cell; papillae were present but were not seen in this view. *M.* Extruded sporangium showing single broad papillae and, within, peripheral layer of zoospores. *N.* A "net sporangium"; all but two zoospores have evacuated their cysts; walls of latter appear as network of polygonal cells. *O.* Two dwarf sporangia. *P.* Zoospores being discharged from sporangium; no evidence of previous encystment of these spores could be observed. *Q.* Zoospores killed with 1 per cent osmic acid and stained with fuchsin. *R.* Portion of "net sporangium" showing partial emergence of zoospore from its cyst. *S.* Sporangium with two open discharge tubes, showing peripheral layer of spores. (*Q*, $\times 800$; *R*, $\times 575$; all others, $\times 235$.)

(Sparrow, 1934c)

(*loc. cit.*) on the zoospores indicated that they were negatively phototactic.

The presence of a net sporangium in *Eurychasma* (Fig. 47 N, p. 530) was believed by Petersen to be of considerable taxonomic import and led him to establish the family Eurychasmaceae. Scherffel (1925a:4) and Coker and Matthews (1937:59) describe this type of spore discharge as *Dictyuchus*-like. The characterization seems hardly accurate, however, since in *Eurychasma* the secondary zoospores never penetrate the sporangium wall, but emerge through the orifice.

IMPERFECTLY KNOWN SPECIES OF EURYCHASMA

? EURYCHASMA SACCULUS H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):477,
fig. VIII, 5, 8-9

Sporangium irregularly saccate, epibiotic part 48-184 μ long, with two short discharge tubes, endobiotic part 40-192 μ long, contorted and lobed, constricted where it passes through the superficial layer of host cells; other characters unknown.

In *Halosaccion ramentaceum*, coll. A. Jessen, *Rhodymenia palmata*, coll. H. P. Sørensen, GREENLAND.

Found most frequently in host cells beneath the superficial layer, rarely in the central cells.

Petersen (conversation, 1933) does not regard the species as distinct from *Eurychasma Dicksonii*. If the lobed nature of the endobiotic part of *E. sacculus* is not due to the action of preservatives, however, this character as well as the nature of the host plants (Rhodophyceae) may separate it from the inhabitant of phaeophyceans.

EURYCHASMIDIUM SPARROW

Biol. Bulletin, 70:241. 1936

(Figure 48, p. 534)

Thallus endobiotic, plasmodial, holocarpic, without a specialized vegetative system, completely or almost filling the distended host cell; sporangium with many discharge tubes which pierce the host wall; zoospores formed within the sporangium, biflagellate, encysting

near the sporangium after discharge, ultimately emerging as motile swarmers; resting spore not observed.

Parasitic in marine Rhodophyceae.

The precise method of entrance of the fungus into the host cell is not known. Magnus (1872:87) states that he observed in one instance that the zoospore came to rest on the wall of the alga, penetrated it, and passed into the contents. Sparrow, on the other hand, presents evidence that the zoospore encysts on the surface and then produces a penetration tube through which the contents pass (Fig. 48 C, p. 534). The subsequent sequence of development is similar to that found in *Eurychasma*, save that the whole body of the fungus with the exception of the tips of the discharge tubes remains endobiotic (Fig. 48 A-G). Further, the zoospores of *Eurychasmidium* encyst outside the sporangium (Fig. 48 H). There is also a marked tendency for infected swollen regions of the algal frond to produce adventitious lateral branches.

EURYCHASMIDIUM TUMEFACIENS (Magnus) Sparrow

Biol. Bulletin, 70:241, text figs. 14-21, pl. 1, fig. 1. 1936

Chytridium tumefaciens Magnus, Sitzungsber. Gesell. Naturforsch. Freunde Berlin, 1872:87; Wissensch. Meeresunters. Abt. Kiel, 2-3:76, pl. 1, figs. 1-16. 1875.

Olpidium tumefaciens (Magnus) Wright, Trans. R. Irish Acad. Dublin (Sci.), 26:360. 1879.

Pleotrichelus tumefaciens (Magnus) H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905(5):456.

Sporangia spherical and 100-110 μ in diameter or irregular, lobed, and 110 μ wide by 200 μ long, from one to six, nearly or completely filling the abnormally enlarged host cell, the alga being stimulated to form clusters of lateral branches in the infected region, wall thin, smooth, colorless; zoospores very numerous, escaping through as many as thirty short narrowly cylindrical sessile discharge tubes, encysting outside, the loosely disposed cysts angular and 4 μ in greatest width, emerging from the cysts after a period of quiescence as ellipsoidal biflagellate zoospores 5 μ long by 3 μ in diameter; resting spore not observed.

Parasitic in *Ceramium flabelligerum*, *C. acanthonotum*, Magnus (*loc. cit.*), SCOTLAND; *Ceramium spiniferum* (coll. Cramer), Magnus

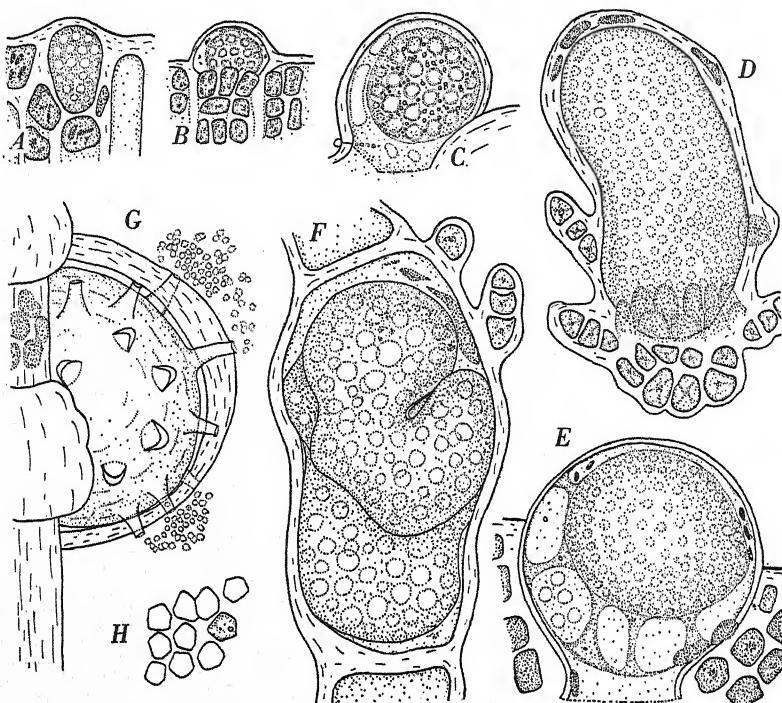


FIG. 48. *Eurychasmidium tumefaciens* (Magnus) Sparrow in *Ceramium diaphanum*

A-B. Early stages in formation of thallus ($\times 225$); host cells are beginning to hypertrophy. *C.* More mature thallus ($\times 376$), showing at bottom of left-hand side the remains of infecting zoospore and its penetration tube. *D-F.* Strongly hypertrophied host cells with vacuolate thalli of fungus in them ($\times 225$). *G.* Empty sporangium showing the many discharge tubes and a few of the discharged, encysted, zoospores ($\times 225$); latter are so numerous as to form a dense cloud around infected region. *H.* Angular cysts produced by discharged zoospores ($\times 760$); all but one cyst is empty.

(Sparrow, 1936b)

(*loc. cit.*), ITALY; *Ceramium acanthonotum*, Wright (1879a:360), IRELAND; "Floridées" (coll. Massart), de Wildeman (1900b:4), FRANCE; *Ceramium rubrum*, H. E. Petersen (1905:456), DENMARK; *Ceramium diaphanum* (coll. C. Jao, Sparrow), Sparrow (1936b:241, text figs. 14-21, pl. 1, fig. 1), UNITED STATES.

The American material was found only in the nodal cells of the

alga. The earliest developmental stages observed showed an already well-established spherical thallus easily distinguishable from the host contents by its numerous irregular refractive bodies. As growth proceeded the disintegrated chloroplast material became more granular, whereas the algal protoplasm assumed a vacuolate character. Coincident with the increase in size of the fungus there was a strong distention of the host cell accompanied by a pronounced thickening of the wall. In addition, certain adjacent nodal cells were stimulated to divide, and there was produced in the vicinity of the infected cell a number of curved stunted lateral branches which gave a "bushy" appearance to the region. Such places could easily be detected with a hand lens. Apparently, some sort of substance was produced in infected cells which diffused to adjacent ones and stimulated them to abnormal growth. Apical cells infected with what was presumably the same fungus showed little hypertrophy.

It is not known whether the myriad of zoospores produced in a single sporangium emerge by action of the flagella or are forced out. Once discharged, they form a dense cloud around the infected part of the filament, each spore being surrounded by an angular wall (Fig. 48 G). These cystospores are not connected with one another as they are in *Eurychasma* but are loosely disposed in the medium (Fig. 48 H). After a varying period of quiescence the protoplasm of each of the cysts emerges, probably through a small pore; it exhibits near the empty shell a rocking motion and undergoes fashioning which terminates with the production of the fully formed biflagellate zoospore. Further observations are needed on the orientation, length, and place of attachment of the two flagella.

The fungus is apparently a true parasite and, unlike certain other marine fungi, does not seem able to continue its destruction of the alga after the latter has been noticeably weakened or killed. The remainder of the host plant, save in the immediate vicinity of the infected cell, appears unaffected by the incursion of the fungus.

Because of the biflagellate character of the zoospores the species cannot be referred to *Chytridium*, *Olpidium*, or *Pleotrichelus*.

APHANOMYCOPSIS SCHERFFEL

Arch. Protistenk., 52:11. 1925

(Figure 49 A-E, p. 537)

Thallus endobiotic holocarpic, branched or unbranched, broad, tubular, one-celled, transformed into a single sporangium; zoospores

diplanetic, the primary spores emerging singly without swarming motion through one or more evacuation tubes and forming at the orifice a cluster of cysts, the secondary zoospores laterally biflagellate, emerging from the cysts through discharge tubes provided at their bases with thick walls which spread apart the valves of the host; resting spores (oöspores?) thick-walled, with eccentric globules and peripheral refractive spots, without periplasm, one or several formed, apparently asexually, in an expanded part of the thallus, germination not observed.

In fresh-water diatoms.

Tokunaga (1934a:232) has proposed the transference of the genus to the Lagenidiaceae on the following grounds: ". . . (1) absence of a typically [well-?] developed mycelium. (2) Thallus completely transformed into the reproductive organs at maturity." While it is unquestionably true that the thallus of *Aphanomyopsis* is of limited extent and that all of it is transformed into a reproductive structure, the method of zoospore formation is markedly different from that found in the Lagenidiaceae, with one exception (noted by Scherffel, 1925a:112). Further, the cytoplasm is typically saprolegniaceous, rather than lagenidiaceous. Then, too, the form studied by Tokunaga is quite different from Scherffel's in that the thallus is septate (see discussion of species below).

APHANOMYCOPSIS BACILLARIACEARUM Scherffel

Arch. Protistenk., 52:14, pl. 1, figs. 31-35, pl. 2, figs. 36-48. 1925

Sporangium 6-10 μ in diameter, unbranched or, more frequently, richly branched, the branches of variable length, discharge tubes one or several, slightly tapering, up to 240 μ long; cysts of the primary zoospores variable in number, 8-10 μ in diameter, secondary zoospores grape-seed-like in shape, 10-12 μ long by 7-8 μ broad, anterior flagellum short and active, posterior one long and passive, movement even, in a zigzag line; oöspores one or several, lying loosely in an expanded part of the thallus, spherical (20 μ in diameter) or broadly ovoid (24 \times 20 μ), colorless, wall thick, smooth, germination not observed.

Parasitic in *Pinnularia viridis*, *Epithemia turgida*, rarely in *Cymbella gastrooides*, *Nitzschia sigmoidea*, Scherffel (*loc. cit.*), HUNGARY; *Pinnularia* sp., Sparrow (1933c:530, pl. 49, fig. 14), UNITED STATES; *Synedra* sp., Sparrow (1936a:461), ENGLAND.

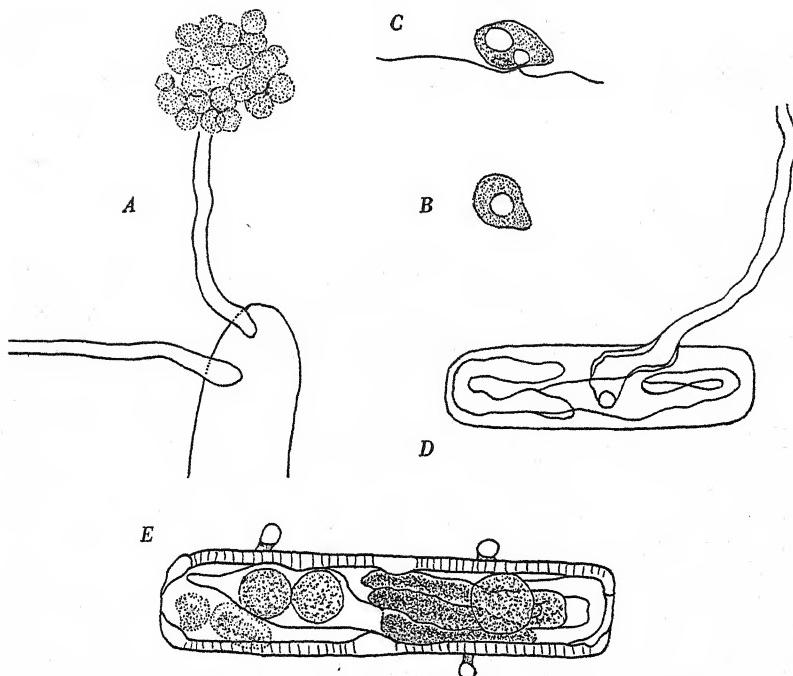


FIG. 49. *Aphanomylopsis Bacillariacearum* Scherffel in diatoms

A. Two discharge tubes emerged from a frustule of *Pinnularia* ($\times 375$), one with a group of encysted primary zoospores. B. Cyst of primary zoospore from which secondary zoospore is beginning to emerge. C. Side view of secondary zoospore. D. Diatom cleared to show endobiotic thallus, and thick-walled "forcing apparatus" at base of long extramatrical discharge tube. E. Diatom on outer surface of which are three encysted zoospores; within a somewhat swollen tubular rudimentary oögonium are two immature oöspores, and a third oöspore to the right is partly masked by disintegrating host contents.

(Scherffel, 1925a)

Tokunaga (1934a:230, fig. 3 a-c) has identified with this species a parasite of diatoms in Japan which, though resembling it in its sporangial stage and resting spore, differs in two important features: (1) in having a septate thallus and (2) in lacking the *Spriezapparat*, or thick-walled spreading apparatus at the base of the evacuation tube which forces the valves apart.

Because of its septate thallus his fungus cannot be included in the Ectrogellaceae as defined by Scherffel (1925a:6) and probably repre-

sents the type of a new genus. Tokunaga's description is quoted here:

Thallus endobiotic, at first consisting of a cylindrical, unbranched tube, later richly branched, provided with long or short, often somewhat inflated twigs, septate at indefinite intervals into a number of cells at maturity, without prominent constriction at the septum, each component cell functioning as a sporangium or an oogonium; sporangia cylindrical or tubular, unbranched, or irregularly branched, often lobed, widely variable in length, up to 150μ long, $4.8-16.8 \mu$ in diameter; exit-tubes single for a sporangium, very long, up to 150μ in length, about 4.8μ in breadth; zoospores on leaving the sporangium coming to rest at once in a hollow sphere at the mouth of the exit-tube, encysting there as in *Achlya*, later swimming away leaving their cyst behind, in encysting globular, $6-7.2 \mu$ in diameter, in swimming kidney-shaped, narrower in front, provided with two cilia near the hilum, containing an oil drop; oogonia (?) intermixed with sporangia in a thallus, terminal or intercalary, cylindrical, medially expanded, $15.6-21.6 \mu$ in breadth, provided with no periplasm; antheridia absent; oospores (?) one or two, lying loosely in an oogonium, spherical, $14.4-19.2 \mu$ in diameter, with smooth, thick membrane and a large oil globule, germination unknown.

Tokunaga's fungus occurs on *Surirella* sp. and *Navicula* sp., JAPAN.

The septate fungus figured by West and West (1906:99, pl. 11, fig. 9) on *Pleurotaenium Ehrenbergii* in Ireland and the Outer Hebrides is probably identical with Tokunaga's fungus. West and West say that it was this fungus which caused Archer (1860:215) to claim that zoospores were formed by desmids.

THRAUSTOCHYTRIACEAE

Thallus epi- and endobiotic, monocentric, eucarpic, chytridaceous in character, the epibiotic part forming the sporangium, the endobiotic part, the vegetative system; zoospores formed in the sporangium, liberated as nonflagellate bodies upon the bursting of the wall, becoming laterally biflagellate; resting stage not observed.

So far as is now known, the family contains but a single genus, *Thraustochytrium (proliferum)*, a saprophyte on marine algae.

This fungus is placed in the *Saprolegniales* on the basis of the biflagellate character of its zoospores. Further resemblances are

to be found in the internal proliferation of the sporangium and in the behavior of the zoospores, which exhibit after their *Thraustotheca*-like discharge a pronounced tendency toward diplanetism. Indeed, it would not be surprising to find upon further investigation that actual encystment of the spores had occurred prior to motility.

THRAUSTOCHYTRIUM SPARROW

Biol. Bulletin, 70:259. 1936

(Figure 46 D-F, p. 524)

Thallus epi- and endobiotic, monocentric, eucarpic, consisting of the epibiotic rudiment of the sporangium derived from the enlarged body of the encysted zoospore and the endobiotic unbranched or branched rhizoidal vegetative system; sporangium liberating the spores upon the bursting and dissolution of the distal part of the wall, internally proliferous; zoospores formed within the sporangium, liberated as nonflagellate, somewhat angular bodies, becoming flagellate after a period of rest, the flagella oppositely directed and apparently anteriorly attached; resting spore not observed.

A monotypic genus known only as a saprophyte on marine algaee.

The establishment and development of the thallus are of the *Chytridium* type (see p. 25).

Recent observations in hanging-drop cultures have revealed important facts about the behavior of the motionless spores after discharge. It has been found that approximately three hours after liberation the individuals in the clumps of freed spores separate from one another. Individual movement of the spore body is initiated, and it loses its angular shape and becomes more ellipsoidal. After a few preliminary twists it then leaves the group as a free-swimming body. The motile spore is somewhat gibbose-pyriform, with a small refractive anterior granule and a central vacuole. Movement is of a slow even character rather than hopping and chytridiaceous. No evidences of encystment of the zoospore during the period of quiescence succeeding discharge can be found.

A further peculiarity of *Thraustochytrium* is its method of internal proliferation. After cleavage of the zoospores (Fig. 46 E, p. 524) there can generally be seen in the sporangium a larger basal protoplasmic unit. This persists after spore liberation, enlarges, and becomes the new, secondary, zoosporangium (Fig. 46 D). Thus, in contrast to the proliferating sporangia of *Saprolegnia*, *Pythiomorpha*,

and so on, the rudiment of the secondary sporangium of *Thraustochytrium* appears to be delimited at the time of zoospore cleavage in the primary body rather than after discharge of the spores (Fig. 46 E-F). Furthermore, it is formed as part of the contents of the primary sporangium, not as an outgrowth from the base. The subsequent enlargement of the secondary sporangium undoubtedly occurs as a result of materials received from the vegetative system.

The small size of the structures involved makes observations on *Thraustochytrium* susceptible to error, and new investigations of this interesting fungus, whose body form appears to exhibit an evolution parallel to that of such true chytrids as *Rhizophydium* and *Chytridium*, are greatly needed.

THRAUSTOCHYTRIUM PROLIFERUM Sparrow

Biol. Bulletin, 70:259, text figs. 22-28, pl. 1, fig. 2. 1936

Sporangium sessile, obpyriform, 15.6-18 μ high by 10-13 μ in diameter, very thin-walled, smooth, colorless; rhizoid branched or unbranched; zoospores few, somewhat angular at liberation, later more spherical, 4 μ in diameter, when motile gibbose-pyriform and 3 μ long by 2.5 μ wide, with an anterior refractive colorless granule and two flagella, movement an even swimming; resting spore not observed.

Saprophytic in *Bryopsis plumosa*, *Ceramium diaphanum*, UNITED STATES.

The zoospores are strongly attracted by the disintegrating chlorophyll of the *Bryopsis* and swarm around the outside of the portions of the cell containing it. As a result, dense clusters of sporangia may be formed in these regions. New observations seem to show that the rhizoidal system is more extensive than was first supposed.

SAPROLEGNIACEAE

Thallus eucarpic, mycelial, without constrictions, of unlimited growth, bearing numerous reproductive organs, homo- or heterothallic; zoosporangia varied in character, usually terminal; zoospores mono- or diplanetic, the secondary zoospores sometimes capable of repeated emergence; antheridia from one to many, androgynous or di-

clinous, sometimes nonfunctional or entirely lacking; oögonium with smooth or pitted wall, eggs from one to many, formed from the entire contents of the oögonium; öospores sexually or apogamously formed, thick-walled, partly or nearly completely filling the oögonium, upon germination forming hyphae or a hyphal stalk bearing a zoosporangium.

Primarily saprophytes of plant and animal debris in fresh water or damp soil; some species parasitic on microscopic and macroscopic animals (fish, amphibia) and roots of higher plants.

The following key is taken from Coker and Matthews (1937) and is included primarily to illustrate the bases on which the genera are separated. Descriptions of the American species will be found in the paper by these authors.

KEY TO THE GENERA OF THE SAPROLEGNIACEAE

Spores monocystic and monoplanetic, their form as in the first swimming stage of *Saprolegnia* 1. PYTHIOPSIS
Spores not as above

Sporangia rare or lacking; spores very variable in behavior, with or without a swimming stage; oogonia with very thick pitted walls; antheridia arising from immediately below the oogonia

2. APLANES

Sporangia, spores, oogonia, and antheridia not as above in all respects

Spores not encysting within the sporangium, normally all emerging from an apical mouth

Spores dicystic and diplanetic

Spores in more than 1 row in the sporangium

New sporangia formed within empty old ones (many exceptions in *S. parasitica*, which approaches *Isoachlya*) 3. SAPROLEGNIA

New sporangia formed for the most part by cymose branching 4. ISOACHLYA

Spores in only 1 row in the sporangium 5. LEPTOLEGNIA

Spores dicystic and dimorphic, but the first swimming stage largely or wholly suppressed

Sporangia not composed of lobulate inflated segments

Spores in more than 1 row

Spores all normally encysting at the mouth of the sporangium 6. ACHLYA

Spores some of them encysting at the mouth of the sporangium but others swimming a short distance before encysting; tip of sporangium rounded and not tapering; proliferating cymosely (usually) but at times internally as in *Saprolegnia* 7. PROTOACHLYA

Spores in 1 row

Branches many of them modified to form spikes which catch and parasitize rotifers

8. SOMMERSTORFFIA

Branches not in the form of spikes 9. APHANOMYCES¹

Branches [sporangia] composed of lobulate inflated segments 10. PLECTOSPIRA

Spores encysting within the sporangium and with or without a swimming stage

Oogonia usually with more than 1 egg

Spores liberated intermittently from the tip of the sporangium which opens by an apical cap ... 11. CALYPTRALEGNIA

Spores leaving the sporangium by the breaking down of the sporangial wall (see also *Achlya dubia*)

12. THRAUSTOTHECA

Oogonia with only 1 egg (oogonia often lacking in *Dictyuchus monosporus*)

Mycelium of vigorous and extensive growth, about as in *Achlya*; spores as a rule not in a single row 13. DICTYUCHUS

Mycelium of very limited growth, dense and opaque

Spores variable in size, but the majority not more than 15 μ thick (some may be elongate), in 1 or more rows; cyst-wall thin 14. BREVILEGNIA

Spores in majority more than 15 μ thick, multinucleate, never swimming, all in single rows; cyst-wall thick 15. GEOLEGNIA

¹ See also *Hydatinophagus*, Valkanov (1931b) and Bartsch and Wolf (1938).

LEPTOMITALES

THE establishment of the Leptomitales as an order coequal with the Saprolegniales has taken place relatively recently (Kanouse, 1927). As here understood, it embraces the family Leptomitaceae of Schroeter (1893) and Minden (1915), exclusive of *Blastocladia* and *Gonapodya*.

The Leptomitales, in which two families are recognized, the Leptomitaceae and the Rhipidiaceae, are all saprophytic fresh-water fungi which usually form tangled or flocculent mats of hyphae or small whitish pustules on the substratum. They occur primarily on vegetable debris, particularly twigs and fruits. Some species seem to prefer cool clear water, whereas others, members of *Rhipidium* and *Leptomitus*, for example, may be found growing under exceedingly foul environmental conditions. The pustules are occasionally composed of a single species of fungus, but more often they consist of a mixture of other Phycomycetes, such as *Blastocladia* and *Gonapodya*. Most species of the order appear, from published records, to be of infrequent occurrence.

The fungi belonging to the genera composing the order form a rather closely related group possessing well-marked structural and reproductive characters in common. Generally speaking, these are the presence of a more or less well defined basal cell, segmentation of the thallus, cellulose walls, pedicellate reproductive structures, and oögamous sexual reproduction. As Miss Kanouse (1927), in establishing the order as distinct from the Saprolegniales, has pointed out, the members of the Leptomitales show definite affinities with the Saprolegniales on the one hand and the Peronosporales on the other. In common with the Saprolegniales they lead an aquatic life, they have the same general thallus structure, and they form numerous zoosporangia which produce biflagellate zoospores. Furthermore, as in the Saprolegniales, the zoospores of two genera of the Leptomitales (*Leptomitus* and *Apodachlya*) exhibit diplanetism or show well-marked evidences of it (Zopf, 1888; Coker, 1923). The Leptomitales resemble the Peronosporales in the nature of their reproductive organs and processes, but are unlike them in habitat and in their lack of parasitic tendencies. As in the Peronosporales, the members of

the Leptomitales (with one exception) form a single oöspore in the oögonium. Except in *Apodachlya* the contents of the oögonium are differentiated into oöplasm and periplasm, and a coenocentrum is distinguishable in the oöplasm (Kevorkian, 1935). In the Rhipidiaceae a functional antheridium is formed which is applied at a definite region on the oögonial wall, and a well-defined, functional fertilization tube is produced.

Zoospores of the primary type are formed in *Leptomitus* and *Apodachlya brachynema*. These encyst, as in *Saprolegnia*, and give rise to swarmers of the secondary type. In the Rhipidiaceae the primary stage is apparently completely suppressed and only secondary zoospores are produced, a further point of resemblance to the Peronosporales.

In spite of the fact that the body structure of members of this order is obviously similar to that found commonly in the Blastocladiales (strikingly exemplified by a comparison of *Blastocladia Pringsheimii* with *Mindenella spinospora*) and in the Monoblepharidales (as illustrated by the segmented hyphae of *Gonapodya* and *Apodachyla*), there is abundant evidence to show that there is no close relationship between them. This is indicated primarily in the structure of the zoospore, the aspect of the protoplasm, the composition of the walls, and the radically different methods of sexual reproduction. These dissimilarities are apparent when the diagnoses of the three orders are compared (cf. pp. 412, 458, and 561). Here again it can be pointed out that a resemblance in the body plan of various fungi has given rise to faulty ideas of relationships.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

The thalli of the two families of the order are unlike in certain features, particularly in the degree of differentiation of the basal cell and the extent of the development of the hyphal branches.

In the Leptomitaceae there appears to be little or no specialization of the proximal portion of the thallus; further investigation of this feature is desirable, however. Apparently no specialized system of holdfasts anchors the plant to the substratum, although Dangeard (1890-91b:120) briefly mentions that such structures are formed in *Leptomitus*. The hyphae of members of this family are well developed and seemingly have unlimited powers of continued growth and

branching. They are conspicuously constricted at more or less regular intervals (Fig. 52 E, p. 566), the constrictions being partly plugged by pseudosepta consisting of a somewhat refractive material termed "cellulin" by Pringsheim (1883a). These constrictions of the main hyphae, and of the branches which may arise immediately beneath them, give a characteristic jointed or segmented appearance to the whole thallus. The contents, at least in *Apodachlya*, are rather lustrous and, in both this genus and *Leptomitites*, possess occasional conspicuous refractive discs of cellulin. These discs, according to Radais (1898), may sometimes act as "corks" to plug up accidental tears in the hyphal walls.

In the Rhipidiaceae the thallus is always somewhat arborescent and more or less strongly differentiated into a basal cell, derived from the body of the germinated zoospore (Minden, 1916), and into hyphal branches which arise from its distal portion (Fig. 53 C, p. 578). The basal cell is anchored in the substratum by a system of tubular, sometimes locally expanded holdfasts. These evidently perform the same function as the rhizoids of the Chytridiales and Blastocladiales, that is, anchorage and absorption, but they appear to lack the characteristic strongly tapering "chytrid-like" aspect. In some species the basal cell may be slender and scarcely differentiated from the hyphae, as in *Sapromyces* (Fig. 53 A'). In others, such as *Rhipidium*, it may be very trunklike, with a "monstrously developed," strongly expanded, lobed and gnarled distal part which forms a platform from which the hyphae and reproductive organs arise. The walls of the basal cell are frequently of considerable thickness, colorless or somewhat brownish (especially with age), and occasionally roughened on the outer surface (Kanouse, 1927). Whatever the extent of development of the basal apparatus, the hyphae arising from it (except in *Mindenella*) are always marked off at their point of origin by a constriction containing a more or less well developed pseudoseptum of cellulin. As in the Leptomitaceae, these hyphae have occasional constrictions along their length (Fig. 53 A). They may remain simple or be sympodially branched.

This curious differentiation of the thallus into rootlike holdfasts, trunklike basal cell, and branches is clearly evident in *Rhipidium* and *Araiopora*, and to a lesser degree in *Sapromyces*. Although branches are lacking in *Mindenella* (Fig. 55, p. 589), the holdfast and basal-cell development is as pronounced as in the other three genera (Kanouse,

1927; Sparrow and Cutter, 1941). Why this particular arborescent habit of growth should appear in wholly unrelated groups of aquatic Phycomycetes is as yet little understood. It can be assumed, however, that such differentiation of the thallus is well adapted to the type of substratum on which all these fungi are commonly found, namely, somewhat spongy decaying fruits and twigs.

REPRODUCTION

Nonsexual Reproduction

In nonsexual reproduction the zoosporangia are formed either singly or in whorls or umbels. In all instances they are separated from the vegetative part of the plant by a constriction within which there is a cellulin plug. For this reason they appear to be resting on a short pedicel. In *Leptomititus* (Pringsheim, 1883a; Coker, 1923), slightly modified segments of the hyphae are simply transformed into sporangia, the terminal one maturing first, and then others in basipetal succession (Fig. 52 A, p. 566). In the remaining genera, however, the sporangia are well-defined broadly or narrowly ovate structures. They are smooth-walled in all except *Araiopora* and *Mindenella*. In these genera sporangia ornamented with spines, as well as the more common smooth-walled type, are formed (Fig. 53 E-F, H, p. 578). In *Mindenella* (Kanouse, 1927; Sparrow and Cutter, 1941), the spiny sporangia (Fig. 55 B, D, p. 589) have a tendency to appear after the colonies have become well established on the substratum, which suggests a possible relationship to the amount of nutrition available. They give rise to the same kind of zoospores as do the smooth-walled sporangia.

The zoospores are cleaved out within the sporangium in a manner similar to that in the Saprolegniaceae. Considerable differences are apparent between the members of the Leptomitaceae and the Rhipidiaceae with respect to the type of zoospore produced at discharge and its subsequent behavior. In the Leptomitaceae definite evidences exist for the diplanetic nature of the zoospore. Thus, in *Leptomititus lacteus* and *Apodachlyta brachynema* the first swimmers to emerge are of the primary, apically biflagellate type (Hartog, 1886-87; Coker, 1923) (Fig. 52 B, I, p. 566). These quickly come to rest and encyst, and from each cyst a laterally biflagellate "secondary" zoospore eventually arises (Fig. 52 J-K). In *A. pyrifera* (Zopf, 1888), however, there is a pronounced tendency for the immediate

encystment of the primary swarmers at the orifice of the sporangium (Fig. 52 E). In the Rhipidiaceae the primary swarm stage is apparently suppressed, although it is possibly represented by the exceedingly ephemeral vesicle which is sometimes formed (Thaxter, 1896b) (Fig. 54 B, p. 582). The zoospores of this family are exclusively of the laterally biflagellate type (Fig. 54 F). There have been no reports except in *Mindenella* (Sparrow and Cutter, 1941) of the repeated emergence of the secondary zoospores.

The zoospores of most species of the order show no unusual features. In *Araiopora spinosa*, *Rhipidium*, and *Mindenella*, however, they are unique and striking objects by reason of the presence within the contents of great numbers of colorless refractive globules (Fig. 54 F, p. 582; Fig. 55 C, p. 589). The body of the zoospore, although differing somewhat in the various genera, conforms for the most part to the "kidney-shaped" or "bean-shaped" configuration common to all zoospores of the secondary type. The flagella are apparently of equal length, oppositely directed, and attached in a shallow groove.

Sexual Reproduction

Sexual reproduction is known to occur in the majority of species. It is apparently lacking, however, in *Leptomitites lacteus*, *Rhipidium parthenosporum*, and *Mindenella spinospora*, the oöspore in the last two genera being supplanted as the resting structure by a parthenogenetically developed resting spore (Kanouse, 1927). Where known, sexual reproduction is oögamous. The oögonia originate in the same manner as the zoosporangia and either terminate hyphal segments or are borne on the basal cell on short pedicels. Except in the aberrant species *Apodachlyella completa* (Humphrey, 1893; Indoh, 1939) only a single egg is formed in the oögonium. In the Leptomitaceae the contents of the oögonium are not differentiated into periplasm and oöplasm, as in the more highly evolved Rhipidiaceae.

The type of sexual reproduction found among members of the Leptomitaceae appears less highly specialized than that among the Rhipidiaceae. In *Apodachlya brachynema* (Coker, 1923; Sparrow, 1932b), which is characterized by the production of numerous lateral moniliform branches, the oögonium arises as a terminal outgrowth of the most distal segment of the branch. This continues to increase in size by the flow of materials to it from the proximal segments. At

maturity it is a large globular structure filled with dense homogeneous mottled protoplasm and subtended by the hypogynous cell from which it had its origin. Like the oögonium, the smaller subterminal cell contains densely granular protoplasm. A light spot (probably a pore) now appears in the base of the oögonium and the contents of the hypogynous antheridial cell slowly pass into the female gametangium. After a short rest period this bright spot disappears and the contents of the fertilized egg become organized into a typical saprolegniaceous oöspore. The wall thickens and one or more oil globules are formed. The oöspore, together with its attendant antheridial cell, may frequently be abscised from the remainder of the thallus. The mature resting structure, the wall of which is distinctly thickened, nearly or, more often, completely fills the oögonium (Fig. 52 C, p. 566). Miss Kanouse (1927:338) has described the oöspore wall of *A. brachynema* as consisting of three parts, an outer and an inner thin layer, and a middle thick one. In *A. punctata* the wall is punctate as in the resting spore of the Blastocladiales (Minden, 1912 [1915]; Sparrow, 1933c) (Fig. 52 G-H). A more specialized antheridium is formed in *A. minima* (Coker and Leitner, 1938). Here the hypogynous cell gives rise to a branch, the tip of which is applied to the oögonium (Fig. 52 D). The cell and the branch continuous with it function as an antheridium. No fertilization tube is formed. Germination of the oöspore of *A. brachynema* by several multinucleate germ tubes has been mentioned by Kevorkian (1935), but no details were given. Coker and Leitner (*loc. cit.*), who have followed the process as it occurs in *A. minima*, describe it essentially as follows: At the inception of germination the contents of the oöspore gradually become granular throughout, with the exception of the large oil droplet, which persists. The oöspore enlarges and cracks open the surrounding oögonial wall. One or two somewhat irregular thick germ tubes protrude through the wall of the oöspore. These tubes elongate, become constricted at intervals, and eventually establish the new mycelium. A plug is formed in the first constriction which prevents the backflow of materials into the now empty oöspore. Frequently the oöspore after cracking open the oögonial wall slips out of its container and falls to the bottom of the culture dish.

In *Apodachlyella completa*, Humphrey (1893) and, more recently, Indoh (1939) have shown that sex organs of a most peculiar type are formed (Fig. 52 F, p. 566). The contents of the oögonium

divide into from two to twelve (usually from four to seven) oöspheres, which eventually become oöspores. The suboögonial segment gives rise to from one to three branches, which are constricted and segmented like the ordinary vegetative hyphae. The terminal segment functions as the antheridium and is applied laterally to the wall of the oögonium. The contents then fragment into from four to ten small spheres, each of which produces a short germ tube and simulates a germinating zoospore. According to Indoh, these tubes penetrate the antheridial and oögonial walls and accomplish fertilization. It is not clear whether all the antheridial spheres discharge their contents into the oögonium. Indoh's observations on this extraordinary phenomenon closely follow those of Humphrey. The latter noted, however, that although the tubes usually grew toward the oögonium there were occasional exceptions, which appear from Indoh's figures to have been present in his material also. These exceptions, together with the occurrence of a few empty terminal segments devoid of such cysts and tubes, led Humphrey to suspect that his material was parasitized.

The sex organs of the Rhipidiaceae are in several ways more highly specialized than those of the Leptomitaceae. The oögonium always bears a single egg, the contents of which during maturation are strongly differentiated into a large somewhat dense mass of oöplasm and a thin vacuolated peripheral layer of periplasm. A single well-defined antheridium is formed which is usually fairly constant as to its point of application to the oögonial wall and which always produces a conspicuous fertilization tube. The wall of the oöspore is generally roughened or ornamented, presumably by periplasmic material.

The oögonia originate singly or in whorls in the same manner as the zoosporangia. They are frequently distinguishable from the latter, however, by their more spherical shape. A constriction is always present beneath the oögonium which divides it from its concomitant hypha. After the oögonium has received its complement of protoplasm and nuclei from the thallus it is separated by a plug of wall material. Details of the protoplasmic changes which then occur are discussed under "Cytology" (p. 552). The antheridium in some species is monoclinous; in others, diclinous. It is borne at the tip of a more or less extended slender branch, and its broad apex is applied to a well-defined spot on the oögonial wall. A cross wall separates

the expanded antheridium from the slender sometimes branching hypha which bears it. The oöspore proper never completely fills the oögonium. It has an inner smooth wall of moderate thickness and an outer one derived from the periplasm. In *Rhipidium* (Fig. 54 C, p. 582) this outer wall is folded into a series of anastomosing ridges which give it an irregular stellate appearance, whereas in *Sapromyces* (Fig. 53 B, p. 578) the wall is almost but not completely smooth, the degree of undulation differing with the species. The oöspores of *Araiopora* (Fig. 53 D, G) are striking objects. Here the living contents, bearing one or more brilliantly golden globules, are surrounded by a thick smooth wall, which in turn is enveloped by a single layer of thin-walled hexagonal cells. Germination of the oöspores has not been observed in any members of the family.

An interesting series of investigations of sexuality in one of the Rhipidiaceae, *Sapromyces elongatus*, has been carried on by Jordan (in Weston, 1938) and Bishop (1940). The almost complete agreement among the relatively few observers of this species that its antheridia were diclinous in origin (Fig. 53 B, p. 578) naturally raised the question as to whether or not it was actually heterothallic in the sense in which that term had been applied to the Mucorales (Blakeslee, 1904). Preliminary studies by Jordan on single isolated basal cells of either oögonial or antheridial plants showed that when these were transplanted to sterile water cultures baited appropriately and grown alone no sex organs were produced. There was, however, one exception, a female strain which formed oögonial initials. When sterile plants, developed from isolated male and female basal cells, were placed in the same culture in such a manner that their branches were interwoven, an abundance of sex organs resulted. Plants forming antheridia could be traced to male basal cells, whereas those forming only oögonia had developed from the female basal cells. In addition to the aberrant female strain previously mentioned, certain of Jordan's gross cultures were composed of strains which never produced sex organs. Some of these when isolated and paired with strains of known sexual potentiality proved to be male, others, female, but there remained a few which showed no sexual potentiality whatsoever. Jordan's preliminary work, therefore, established experimentally what had been suspected as being the reason for the sterile strains reported from time to time by various investigators and so frequently found in nature, that is, that *S. elongatus*, like *Dictyuchus*

of the Saprolegniaceae (Couch, 1926b), was heterothallic. It also showed that there existed in nature a female strain which could form oögonial initials without contact with the opposite sex, as well as other strains which under ordinary conditions showed no reactions to either sex.

Bishop (1940), starting from single-zoospore isolations, extended the study of this fungus and grew it in pure artificial culture. Thirty-nine pure cultures derived from single zoospores were obtained. Of these, seventeen were intensively studied. Four were found to be strongly male and could be distinguished not only by the formation of antheridial branches but by their greater rate of growth. One was classified as "weakly male," five were neuter or neutral, one "weakly female," and six "strongly female." The strongly male and strongly female strains when mated formed reproductive organs (the former, antheridia, the latter, oögonia); the eggs were fertilized, and normal oöspores were developed. There was some evidence that the formation and direction of growth of the antheridial branches were positive responses to substances diffusing from the female; this suggests a hormone action similar to that found in *Achlya* by J. Raper (1939a, 1939b). Evidence derived from various combinations indicated also that, whereas the male strains never showed signs of latent femaleness when grown alone, all female strains under such conditions exhibited undoubted latent maleness, could form antheridial branches, and could even fertilize their own oögonia. Since all the cultures used for critical experimental work were derived from single zoospores, which have been shown by Kevorkian (1935), using cytological methods, to be uninucleate, the older theory postulating that each nucleus possesses the potentialities of but one sex could not be applied here to explain the sexual phenomena found in *Sapromyces elongatus*. On the basis of the results of these investigations Bishop concluded that the theory of "relative sexuality" proposed by Hartmann (1925), rather than the "heterothallism" of Blakeslee, best explained the observed facts. He pointed out that heterothallism implied the strict unisexuality of the individual, whereas relative sexuality postulated that there were:

... even in single nuclei, male potencies (A) and female potencies (G) under the control of male realisators (α) and female realisators (γ). In the male strains of haplogenotypic, heterothallic organisms, the male realisator (α) is at once the means of activation of the male potency (A)

and the inhibition of the female potency (G). The reverse is true in the female strains of such organisms, where the female realisator (gamma) activates the female potency (G) at the expense of the male potency (A)

On this hypothesis Bishop has indicated that the following types of sexuality may be present in *S. elongatus*: pure male (*MM*), male with latent femaleness (*Mf*), neutral, strongly sexed (*MF*), neutral, weakly sexed (*mf*), female with latent maleness (*mF*), and pure female (*FF*). Of the seventeen single-zoospore cultures studied by Bishop, there were five of the *MM* type, seven of the *mF* type, and five of the *mf* type. He suggests that further collections may reveal the *FF*, *Mf*, and *MF* types.

CYTOTOLOGY

Representatives of all genera of the Leptomitales save *Mindenella* have been studied cytologically, and, consequently, their nuclear behavior is well known.

In the types examined (*Leptomitus lacteus*, *Apodachlya brachynema*, *Sapromyces elongatus*, *Araiopora pulchra*, and *Rhipidium interruptum*) the thallus has been found to be multinucleate, with the nuclei scattered throughout a peripheral layer of cytoplasm lining a central vacuole. Nuclei are especially abundant in the growing apices. Kevorkian (1935) states that the numerous nuclei found in the basal cell of *S. elongatus* result from the repeated mitotic divisions of the single nucleus of the zoospore during its germination. In the basal cell of *Rhipidium*, which is even more developed than that of *Sapromyces*, Behrens (1931) has noted that the many nuclei formed migrate into the developing hyphal branches, which as a result become nucleated.

The nuclei appear to flow with the protoplasm into the rudiments of the zoosporangia, for no division figures have been observed. Once the sporangium attains its full size it is cut off from its attendant hypha by a basal hyaline plug. The nuclei are at first irregularly arranged in the rudiment, but eventually a central vacuole forms, around which, at least in certain species, they become regularly disposed in one or two layers. Lines of cleavage then extend from the vacuole outward (Behrens, 1931) and divide the contents into uninucleated segments of approximately equal size. These segments, the zoospore initials, become flagellate before their discharge from the

sporangium. The precise method of formation of the delicate whip-like flagella is, however, understandably obscure.

In the motile primary pip-shaped zoospores of *Apodachlya* the nucleus is in the anterior part of the body. The two apical flagella

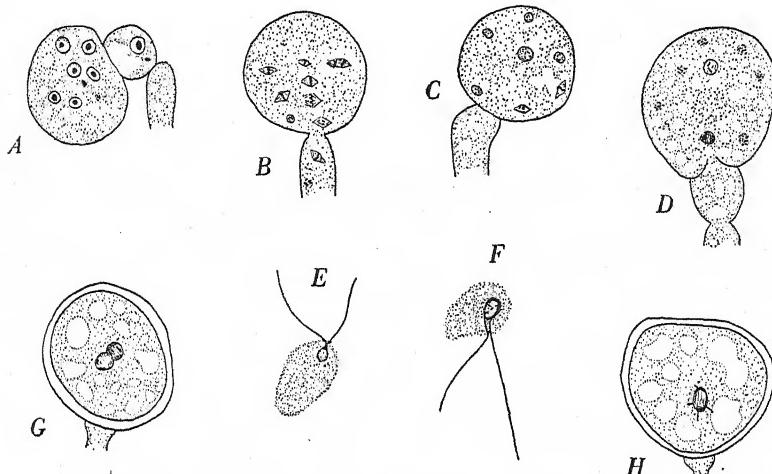


FIG. 50. Cytology of *Apodachlya brachynema* (Hildebrand) Pringsheim

A. Immature terminal oogonium and hypogynous antheridium, showing arrangement of nuclei. B. Simultaneous mitoses in oogonium and antheridium. C. Oogonium with nuclei in peripheral position prior to their degeneration. D. Oogonium and antheridium, showing gamete nuclei and a number of degenerating peripheral nuclei. E. Primary zoospore with the two anterior flagella each connected to a distinct basal granule, which in turn is connected to nucleus by a delicate strand. F. Secondary swarmer, with the two laterally placed flagella each attached to a distinct basal granule, which in turn is attached to nucleus. G. Oogonium with thickened wall (oöspore?), with the two gamete nuclei closely associated but not yet fused. H. Oogonium bearing nearly completely fused nuclei, from which a few astral rays emanate. (A-D, G-H, $\times 400$.)

(A-D, G-H, Kevorkian, 1935; E-F, Cotner, 1930b)

are connected to separate "basal granules" of nuclear origin (Cotner, 1930b), and these, in turn, by delicate fibrillar structures to the tip of the beaked nucleus (Cotner, *loc. cit.*; Kevorkian, 1935) (Fig. 50 E). The secondary swarmers in all genera of the order appear to be nearly

uniform in internal structure and organization of the nucleus, which is more centrally disposed than in the primary zoospore. In all secondary types of zoospores the nucleus is somewhat beaked. Occasionally two opposite beaks are formed (Cotner, *loc. cit.*). In *A. brachynema* there emerge from the tip of the beak, which is usually darker-staining, either two delicate fibrillar strands or a single one. The latter is supposedly composed of two fused fibrils (Cotner, *loc. cit.*) connecting with basal granules from which the oppositely directed flagella have their origin (Fig. 50 F). In the secondary zoospore of *Rhipidium interruptum* (Cotner, *loc. cit.*) the basal granules are united with a more massive chromatic body which is adjacent to the nucleus. Cotner considers these basal granules of nuclear origin, and intimately connected with the formation and control of the flagella. He points out that they are present wherever flagella are found and that if more than the usual number of granules are formed a corresponding number of flagella appear. He describes the "basal apparatus" as consisting of several granules, two of which usually remain within the nucleus to form its dark-staining beak, whereas the third is on the periphery of the cytoplasm at the base of the flagellum. He also asserts that even though the granules are of nuclear origin, once formed they appear to function even after separation from the nucleus. He thus indicates that the flagella may arise from and be controlled by differentiated parts of the nuclear material rather than by the whole nucleus. The well-coördinated movement of these swarmers through the water seems, however, to indicate that there is some central controlling body, most likely the main body of the nucleus, of which the granules are, after all, an integral part.

It is in the sexual stage that the most interesting nuclear phenomena are to be found. Since members of the two families differ markedly from each other in this phase they will be considered separately.

In the Leptomitaceae sexuality is known in *Apodachlya* and *Apodachlyella*. Only *Apodachlya brachynema*, however, has been investigated cytologically. In this species (Kevorkian, 1935) the oögonium is terminal and the antheridium is the hyphal segment immediately below it (Fig. 50 A, p. 553). The male organ at maturity contains from three to four spherical nuclei which are scattered in the protoplasm. These undergo a simultaneous mitotic division, after which one nucleus enlarges and the remainder degenerate. Mean-

while a simple pore has been formed on the membrane separating the two gametangia, through which the contents pass into the oögonium. No specialized fertilization tube is produced. The developing oögonium possesses at first from ten to twenty nuclei, which have been carried into it by the inflow of protoplasm prior to the formation of the basal septum separating it from the antheridial cell. These nuclei are at first more or less evenly distributed in the protoplasm. When the oögonium achieves its maximum size and is separated from the antheridium a single simultaneous mitotic division of these nuclei occurs. This division is coincidental with that in the antheridium (Fig. 50 B). The nuclei of the two organs may not, however, all be at the same stage of division. All but one of the nuclei in the oögonium make their way, possibly by means of vacuolar activity, to the periphery of the oöosphere. The single favored nucleus assumes a central position and enlarges, attaining ultimately from two to three times its original size ($2.5\text{--}3.5 \mu$ in diameter). The peripheral nuclei then degenerate (Fig. 50 C). A poorly defined irregular coenocentrum surrounds the egg nucleus. The male nucleus, upon its entrance into the oögonium by way of the pore, migrates toward the nucleus of the egg (Fig. 50 D) and makes contact with it. Both then enlarge. A few astral rays emanate from the region of the nuclei. Actual fusion, however, may not take place until the oöspore wall is in the process of thickening (Fig. 50 G-H). No cytological details of germination are given. Reduction division presumably occurs at germination, at which time the multinucleate germ tubes are formed.

In the Rhipidiaceae the sexual process is of a higher type, although the general sequence of nuclear activity is essentially the same as that in *Apodachlya*.

In *Sapromyces elongatus* (Kevorkian, 1935) the oögonia and the antheridia are formed on different branches and usually on separate thalli. The antheridium contains from four to six nuclei, which are similar to those found in the sporangia and the oögonia. These undergo a single simultaneous mitotic division, after which all but one degenerate. Meanwhile a fertilization tube has been developed which penetrates the wall of the oögonium and reaches the oöosphere. One male nucleus is discharged through this tube into the egg. The developing oögonium contains from ten to twelve spherical nuclei, which have been carried into it with the inflowing protoplasm. It

is not clear when the basal cross wall is laid down. The contents of the oögonium become vacuolate, however, and the nuclei undergo a single simultaneous mitotic division. All save one favored nucleus now migrate to the periphery and degenerate. Occasionally degeneration of the supernumerary nuclei may occur without their migration. The gamete nucleus then enlarges and occupies the center of the egg. At some time before fertilization the oögonial contents become differentiated into a large central mass of oöplasm and a thin peripheral layer of periplasm into which the supernumerary nuclei have migrated. The periplasm continues to become less granular than the oöplasm, and a thin membrane eventually separates the two. Evidently during or prior to the delimitation of the inner periplasmic membrane (the time is not mentioned) the male nucleus is discharged into the oöplasm through the fertilization tube. As in *Apodachlya*, a coenocentrum and a few astral rays are developed. Nuclear fusion is delayed, but, from the figures given, it seems to occur before formation of the oöspore wall.

The investigations of King (1903) on *Araiopora pulchra* and particularly those of Behrens (1931) on *Rhipidium interruptum* give the most complete accounts of the cytology of members of the Rhipidiaceae. In *Rhipidium* the oögonium originates in exactly the same fashion as the sporangium, the two structures being indistinguishable at first. About thirty or thirty-five nuclei migrate into the developing oögonium before it is separated from its hypha by a cross wall (Fig. 51 A, p. 558). In the mature oögonium all save one of the nuclei are arranged around the periphery (Fig. 51 B). No single large central vacuole is formed, as is characteristic of the sporangium, but, rather, several large irregularly disposed ones appear.

Each of the nuclei has a fairly prominent dark-stained nucleolus and several dark-stained peripheral granules. Differentiation of the content of the oögonium then ensues. The peripheral material forms numerous polygonal vacuoles, whereas the inner, main content develops a fairly regular meshwork of smaller vacuoles. The supernumerary nuclei are arranged in the protoplasmic meshwork in a thin vacuolate layer of periplasm or between the periplasm and the oöplasm, and the single oögonial nucleus is in approximately the center of the somewhat denser oöplasm (Fig. 51 C, p. 558). There follows an almost simultaneous mitotic division of all the nuclei (Fig.

51 D). The spindles produced during this process have no definite orientation and are intranuclear. After division the periplasm in which the now paired smaller supernumerary nuclei lie becomes more deeply stained. Evidences of nuclear degeneration are apparent. One of the two central nuclei becomes the egg nucleus; the other, like the periplasmic nuclei, degenerates.

The antheridium, the broad apex of which is applied near the base of the oögonium, is cut off from its branch by a cellulose plug (Fig. 51 D, p. 558). It contains about four nuclei. The oögonial wall at the point of application of the antheridium bulges out, papilla-like, possibly because of the slighter resistance of the wall at this point to the internal pressure of the oögonium. This protuberance then springs into a correspondingly formed cavity of the antheridium. Thus the antheridium and the oögonium are brought into intimate contact. Because of the constancy of point of application of the antheridium to the oögonium, Behrens raises the question as to whether or not the female structure emits material attractive to the antheridial branch. The four antheridial nuclei are like those of the oögonium, but stain more intensely. Soon after mitosis has occurred in the oögonium they too undergo a single mitotic division. Only one of the eight nuclei thus formed persists; the remainder degenerate. Soon after this nuclear division the wall of the oögonium dissolves at the point of application of the antheridium, and the antheridium produces a fertilization tube (Fig. 51 E). At the time of entrance of the fertilization tube into the oöplasm there occurs a progressive resorption of the periplasm and an increase in the amount of the deep-staining peripheral oöplasmic material. A delicate membrane is laid down between the vacuolated periplasm with its supernumerary nuclei and the oöplasm. The egg nucleus at this time is as yet unfused with the male nucleus. It possesses a perceptible beak with centrosome-like granules at the tip (Fig. 51 E). Delicate polar rays which extend beyond a darker-stained coenocentrum are clearly visible. Upon the dissolution of the tip of the fertilization tube a single male nucleus is discharged, and this apparently moves fairly quickly to the vicinity of the somewhat larger egg nucleus (Fig. 51 F). The tenuous membrane delimiting the periplasm now becomes continuous, completely separates the oöplasm from the dwindling periplasm, and gradually thickens and becomes doubly contoured, the accretion evidently being derived from the previously mentioned deeper-

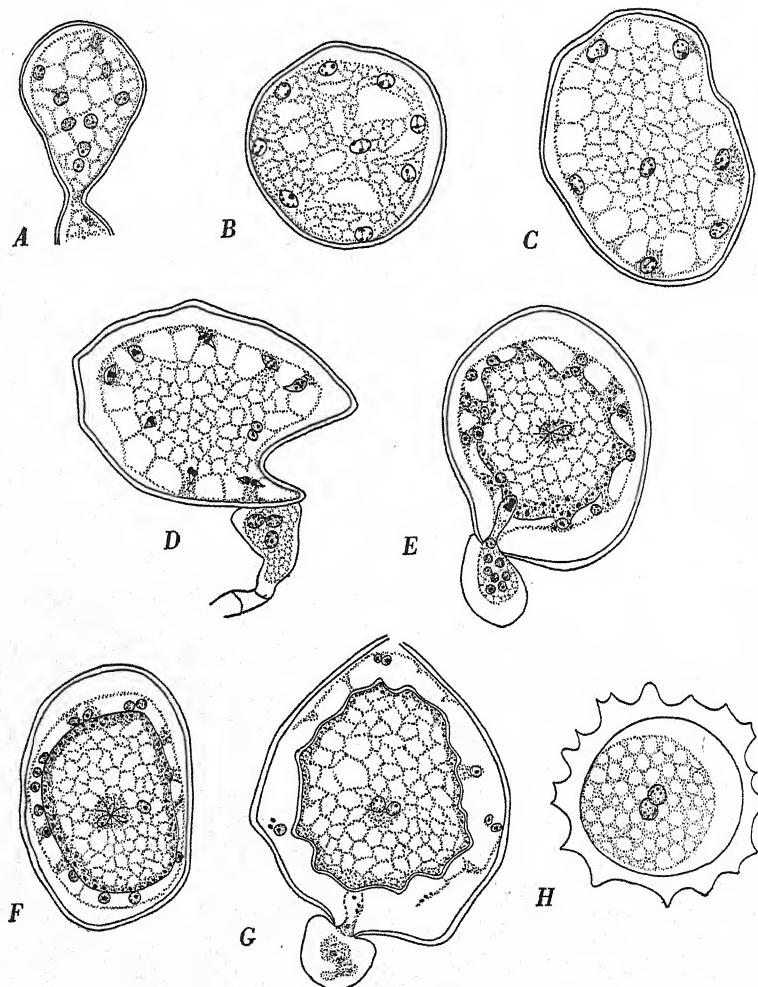


FIG. 51. Cytology of sexual organs of *Rhipidium interruptum* Cornu

A. Young oogonium; cytoplasm is vacuolate and nuclei have already begun to move toward periphery; cross wall has not as yet cut off oogonium from hypha; the two basal, lighter-stained nuclei have probably just recently entered oogonium. B. Mature oogonium; nuclei have all, with one exception, assumed a peripheral position; cytoplasm is alveolate and contains large vacuoles. C. Oogonium shortly before nuclear division; differentiation into periplasm and ooplasm is completed. D. Nuclear division in

stained outer layer of the oöplasm. As the wall thickens, this outer layer slowly decreases. The double contour of the wall is visible even before the rays have vanished from the female nucleus. The residue of periplasm and the supernumerary nuclei then disappear. At the same time the oöspore wall thickens and assumes by unequal accretions, aided no doubt by outside material, its characteristic irregular contour. The irregularities of the oöspore wall are not, however, Behrens says, related to the honeycomb-like original disposition of the periplasm, as Minden and others have asserted. That is, the thin primary wall does not form around both peri- and oöplasms, but originates as an outgrowth from the smooth wall which has been described as lying between the two. During maturation of the oöspore the gamete nuclei remain in close proximity and assume equal size (Fig. 51 G). Not even in the fully mature oöspore was fusion observed (Fig. 51 H). Judging from this, Behrens supposes that karyogamy occurs shortly before germination. Neither of these processes was observed, however.

In *Araiopora* the sexual process and the accompanying nuclear phenomena as described by King (1903) appear similar to those of *Rhipidium*, although differences in interpretation are apparent. Cytoplasm and from thirty to thirty-five nuclei migrate into the developing oögonium, which is eventually cut off by a plug from its hypha. The nuclei pass out along radii of the oögonium and become

oögonium; the three visible nuclei of antheridium have not as yet divided. *E.* Oögonium, showing a single central beaked egg nucleus with a centrosome from which radiate striae; resorption of periplasm is in progress and strongly stained inclusions have made their appearance around periphery of egg; first indications of wall formation are visible; antheridium has produced fertilization tube, its nuclei have divided, and one gamete nucleus has just entered base of tube; deep-staining material at tip of tube indicates that deliquescence of apex has begun. *F.* Oögonium in which male nucleus is shown approaching larger egg nucleus; degeneration of supernumerary nuclei and resorption of periplasm is in progress; dark-staining peripheral material is clearly defined, as is wall. *G.* Egg with large, nearly like-sized, paired male and female nuclei; oöspore wall has taken on its typical contour; periplasm has for most part been resorbed, though occasional periplasmic nuclei still persist, as does fertilization tube. *H.* Mature oöspore; nuclei have not as yet fused. (All $\times 353$.)

(Behrens, 1931)

regularly disposed in a peripheral position. The contents at this time are an undifferentiated cytoplasmic meshwork surrounding large irregular vacuoles. As development proceeds, these vacuoles disappear, and the central region becomes more uniformly vacuolate. Near the periphery other regularly placed vacuoles increase in size until the cytoplasm in this region is coarse-meshed. The nuclei, in the interval, have come to rest in the cytoplasmic strands between the vacuoles. In the central region prominent isolated fine-meshed patches appear. King presumes that these eventually fuse to form the coenocentrum, a structure which possibly helps draw the sex nuclei into proximity with one another. Meanwhile differentiation into oöplasm and periplasm has taken place, and at some time a mitotic division of the nuclei has occurred, although the evidence for this is admittedly scanty. The origin of the nucleus of the female gamete was not observed. To judge from the figures given, it is probable that, as in *Rhipidium*, this nucleus assumes at once a central position in the oögonium. As the oöplasm is cut off from the periplasm, a radial division of the intervacuolar strands of the latter gives rise to a large number of cells. Cell walls are then laid down between adjacent peripheral cells, as well as between these and the central oöplasm.

A receptive papilla is formed from a differentiated portion of the egg, just within the oögonial wall at the point of application of the antheridium. A fertilization tube is produced which King considers to be laid down by periplasmic material, not by the antheridium. This point has been disputed by Thaxter in observations on living plants of the same species, and by Kevorkian in regard to a congeneric form, *Araiopora streptandra*. Behrens, too, concludes from his cytological study of *Rhipidium interruptum* that King was in error, and shows that the fertilization tube in *Rhipidium*, after its tip has deliquesced, gives the appearance of being a canal of oögonial origin. The antheridium contains from five to seven nuclei. From the fact that the older antheridia contained twice this number, it was presumed that here, as in the oögonial nuclei, a mitotic division had occurred. At fertilization a single nucleus is introduced into the egg; the remainder degenerate. While the two sexual nuclei approach the center of the egg (and each other) they become beaked, as though a mutual attraction existed between them. No nuclear

fusion was found, and wholly mature oöspores were always binucleate. Like Behrens, King suggests that karyogamy probably occurs at the close of the rest period undergone by the oöspore.

During the maturation of the oöspore the nuclei increase in size. If, as is usual, a large central reserve globule is formed, they are displaced laterally. Although the point is not clearly brought out by King there is much evidence in the figures given to indicate that in *Araiospora pulchra* the wall of the oöspore proper is formed in much the same manner as was described by Behrens for *Rhipidium*. The cellular envelope, so characteristic of *Araiospora* (Fig. 53 D, F-G, p. 578) but not found in *Rhipidium*, appears to be formed directly from the periplasm.

In a treatise primarily of a taxonomic nature no extensive physiological material is ordinarily dealt with. It might be said, however, that precise knowledge of the metabolic processes and the conditions necessary for growth of members of this order is confined to species of two genera of the Leptomitaceae, *Leptomitus* and *Apodachlyla*. Minden (1916), to be sure, briefly described the growing in culture of species of *Rhipidium* and *Araiospora* in various natural and synthetic media, and more recently Bishop (1940) has indicated something of the nutritional requirements of *Sapromyces elongatus* (S. *Reinschii*), but neither has attempted a comprehensive study or has presented an extensive analysis of his results. Schade (1940) and Schade and Thimann (1940) have made comparative physiological investigations of *Leptomitus lacteus* and *Apodachlyla brachynema*. The more extensive literature pertinent to the physiology of *Leptomitus* is cited in their papers.

SYSTEMATIC ACCOUNT

LEPTOMITALES

MICROSCOPIC saprophytic fresh-water fungi, the thallus with or without a well-defined basal cell and holdfasts, the hyphae divided into constricted pseudocells by pseudosepta of cellulose, walls giving a cellulose reaction; reproductive organs consisting of segments of the

hyphae or specialized pedicellate structures cut off by cross walls and constrictions from the attendant mycelium; zoosporangia forming mono- or diplanetic biflagellate zoospores; oögonia with or without periplasm, forming (except in *Apodachlyella*) a single egg; antheridium either a single segment or borne on specialized branches of mono- or diclinous origin, with or without a fertilization tube; oöspores single (except in *Apodachlyella*), thick-walled, upon germination forming hyphae.

The order erected by Miss Kanouse (1927:295) differs from the Saprolegniales primarily in the division of the thallus into pseudocells by pseudosepta, the pedicellate reproductive organs, and the formation of a single (except in *Apodachlyella*) egg in the oögonium.

KEY TO THE FAMILIES OF THE LEPTOMITALES

Thallus filamentous throughout, not differentiated into a basal cell and hyphal branches; zoospores diplanetic; oögonial contents not differentiated into oöplasm and periplasm

LEPTOMITACEAE, p. 562

Thallus more or less well differentiated into holdfasts, basal cell, and hyphal branches; zoospores of the secondary type; oögonial contents differentiated into oöplasm and periplasm

RHIPIDIACEAE, p. 572

LEPTOMITACEAE

Thallus filamentous throughout, conspicuously jointed and pseudoseptate, of unlimited growth, contents bearing refractive granules of cellulin; zoosporangia either undifferentiated hyphal segments or specialized pedicellate smooth-walled structures; zoospores diplanetic, the primary swarmers apically biflagellate, the secondary laterally biflagellate; oögonium forming one or several oöospheres the contents of which are homogeneous and not differentiated into oöplasm and periplasm, oöspore smooth-walled, at germination forming several germ tubes which reëstablish the thallus; antheridium a relatively unspecialized segment of the thallus which subtends the oögonium, not forming a fertilization tube.

Saprophytic on various types of submerged debris, frequently fruits and twigs, in fresh water.

KEY TO THE GENERA OF THE LEPTOMITACEAE

- Sex organs never formed; plant coarse, the zoosporangia being undifferentiated segments of the mycelium LEPTOMITUS, p. 563
- Sex organs formed under ordinary conditions of culture; plant more delicate, the zoosporangia (if formed) being well-defined pedicellate structures.
- Oögonium forming a single oöspore APODACHLYA, p. 564
- Oögonium forming more than one oöspore APODACHLYELLA, p. 571

LEPTOMITUS AGARDH

Systema algarum, p. 47. 1824

(Figure 52 A-B, p. 566)

Apodya Cornu, Ann. Sci. Nat. Bot., V, 15:14. 1872.

Thallus stout at the base, filamentous throughout, monopodial, dichotomously branched near the base, the hyphae constricted and pseudoseptate at intervals, the branches arising at the constrictions, apparently without specialized holdfasts, each segment containing one or more cellulose discs; sporangia formed from unspecialized segments of the mycelium, terminal or developed in basipetal succession; zoospores formed in the sporangia in one row (occasionally irregularly disposed), diplanetic, the primary spores apically biflagellate, emerging through a terminal or lateral pore, encysting after a period of swarming, secondary spores laterally (?) biflagellate; sexual organs not observed.

Saprophytic on debris, often in heavily polluted fresh waters.

The secondary zoospore is described only as being biflagellate.

LEPTOMITUS LACTEUS (Roth) Agardh

Systema algarum, p. 47. 1824

Conferva lactea Roth, Catalecta botanica, 2:216. 1800.*Leptomitus libertiae* Agardh, loc. cit., p. 49. 1824.*Saprolegnia lactea* Pringsheim, Jahrb. wiss. Bot., 2:228, pl. 23, figs. 6-10, pl. 25, figs. 1-6. 1860.*Apodya lactea* Cornu, Ann. Sci. Nat. Bot., V, 15:14. 1872.*Saprolegnia corcagiensis* Hartog, Quart. J. Micro. Sci. (N. S.), 27:429. 1886-87.

Basal segment stout, up to 48 μ in diameter, branches 8-16 μ in diameter, the segments up to 400 μ in length; zoosporangia cylindrical, formed from slightly swollen segments of the mycelium, pri-

mary zoospores pyriform, 10.5–11 μ in diameter, secondary zoospores biflagellate.

Forming large turflike masses often of great extent on organic debris, particularly in waters with a high organic content, rarely in purer waters. Roth (*loc. cit.*), Agardh (*loc. cit.*), Braun (1851:287), Pringsheim (1860:228, pl. 23, figs. 6–10, pl. 25, figs. 1–6; 1883a: 288, pl. 7, figs. 1–9), Büsgen (1882:266, pl. 12, figs. 9–15), Schroeter (1885:255), Kolkwitz (1901; 1903), Minden (1915:582, fig. 14b [p. 580]), GERMANY; Dillwyn (1809: pl. 79), ENGLAND; Dangeard (1890–91b:118, pl. 6, figs. 24–31), Radais (1898:144), Guilliermond (1922), FRANCE; Humphrey (1893:135, pl. 14, fig. 6), Coker (1923:170, pl. 58), Kevorkian (1935: pl. 19, fig. 10 a–b), UNITED STATES; Tulloch (1934), ALASKA.

Numerous references are found in the older literature to "*Leptomitus*," one of the earliest-studied members of the water fungi, and exsiccati are quoted by Minden (1915:582). Fischer (1892: 371) has discussed these older records. A careful morphological study of this species is greatly needed. Kolkwitz (1903:34), Schade (1939), and Schade and Thimann (1940) have made investigations of the physiology of the organism.

APODACHLYA PRINGSHEIM

Berichte Deutsch. Bot. Gesell., 1:289. 1883

(Figure 52 C–E, G–K, p. 566)

Thallus filamentous throughout, the hyphae constricted and pseudoseptate at intervals, monopodial, often richly branched, the branches arising at the constrictions, apparently without specialized holdfasts, contents faintly refractive, bearing from one to three cellulin discs in each segment; zoosporangia terminal or sympodially arranged along the hyphae, rarely in basipetal succession, pedicellate, ovoid, pyriform, or occasionally cylindrical, zoospores few, diplanetic, primary spores apically biflagellate, formed in the sporangium, encysting at once at the orifice after discharge or swimming directly away, secondary spores laterally (?) biflagellate, emerging from the cysts after a period of quiescence; oögonia borne singly, terminally or laterally, subtended by a linklike antheridial cell, fertilization tube lacking; oöspore thick-walled, with one or more large globules, borne singly in the oögonium, which it nearly or entirely fills, upon germination forming from one to two germ tubes.

The five known species are primarily inhabitants of twigs and submerged fruits.

The slender slightly refractive or gray lustrous filaments are readily distinguishable from the coarser ones of *Achlya*, with which they often occur.

Coker (1923) and Kevorkian (1935) describe the oögonium as lacking periplasm. In the development of the sex organs of *Apodachlya brachynema* Coker observed that the future antheridial cell reached its mature size before the oögonium appeared. The latter was then formed by the enlargement of a small globular outgrowth produced at the apex of the antheridium (see "Sexual Reproduction," p. 547).

KEY TO THE SPECIES OF APODACHLYA

Oöspore smooth-walled, not punctate

Sporangia, if formed, developed singly or in clusters, not in basipetal succession

Oögonia borne at the tips of short moniliform segments; zoospores, if present, rarely encysting at the orifice of the sporangium

Antheridium the suboögonial cell; sporangia formed in abundance *A. brachynema*, p. 565

Antheridium borne on a short lateral outgrowth beneath the oögonium; sporangia not formed *A. minima*, p. 568

Oögonia borne at the tips of the main axes, occasionally laterally, subtended by an antheridial cell; zoospores generally encysting at the orifice of the sporangium

A. pyrifera, p. 568

Sporangia developed in basipetal succession or singly. *A. seriata*, p. 570
Oöspore wall minutely punctate *A. punctata*, p. 570

APODACHLYA BRACHYNEMA (Hildebrand) Pringsheim

Berichte Deutsch. Bot. Gesell., 1:289. 1883

(Figure 52 C, I-K, p. 566)

Leptomitus brachynema Hildebrand, Jahrb. wiss. Bot., 6:261, pl. 16, figs. 12-23. 1867-68.

Apodya brachynema (Hildebrand) Cornu, Ann. Sci. Nat. Bot., V, 15:14. 1872.

Mycelium branched, the segments 20-185 μ long by 4-23 μ in diameter, generally becoming shorter near the sporangia, the lateral

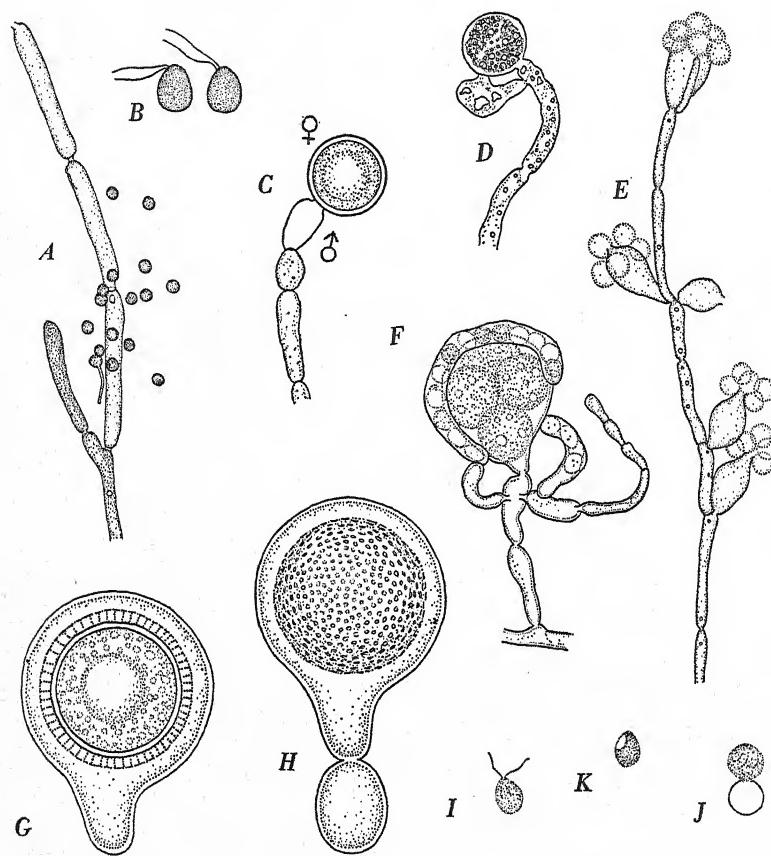


FIG. 52. Leptomitaceae

A-B. Leptomitus lacteus (Roth) Agardh: *A*, portion of plant three of whose segments have discharged their zoospores ($\times 150$); latter have encysted; *B*, zoospores after treatment with iodine ($\times 430$). *C*. Sex organs of *Apodachlya brachynema* (Hildebrand) Pringsheim ($\times 405$). *D*. Sex organs of *Apodachlya minima* Coker and Leitner ($\times 418$). *E*. *Apodachlya pyrifera* Zopf ($\times 250$), portion of plant with encysted zoospores at orifices of sporangia. *F*. *Apodachlyella completa* (Humphrey) Indoh, sex organs. *G-H*. Oöspore of *Apodachlya punctata* Minden ($\times 500$): *G*, optical section, showing structure of wall; *H*, surface view, showing punctations (drawn from a photomicrograph). *I-K*. *Apodachlya brachynema* (Hildebrand) Pringsheim ($\times 405$): *I*, primary, apically biflagellate zoospore; *J*, secondary zoospore

branches mostly distal, often moniliform; sporangia terminal, single or several, sympodially arranged or in clusters, subspherical, ovoid, ellipsoidal, or pyriform, with an apical, subapical, or lateral somewhat prolonged discharge papilla, 23–76 μ long by 23–44 μ in diameter; zoospores from six to twenty, primary spores broadly ovoid, 12–14 μ (long?), apically biflagellate, swimming directly from the sporangium before encysting, cysts spherical, 8.5–10 μ in diameter, secondary zoospores biflagellate; oögonia spherical or broadly pyriform, 23.5–29 μ in diameter, terminal, borne singly at the tips of short lateral moniliform segments, the subapical segment functioning as the antheridium; oöspore single, 20–40 μ in diameter, filling the oögonium, wall smooth, about 1.8 μ thick, contents finely granular, with small regularly disposed globules, a vacuole, and from one to two large eccentric globules, upon germination producing a germ tube(?)

On twigs, Hildebrand (*loc. cit.*), GERMANY; Thaxter (1896b:325), termite, Coker (1923:173, pl. 59), fruits of apple and *Crataegus*, Kanouse (1927:338), Harvey (1930:327), apples and twigs, Sparrow (1932b:296; 1933c:532), UNITED STATES.

Kevorkian (1935:279) mentions that the oöspores of *Apodachlya brachynema* germinate, presumably by a germ tube, but no details of the process are given. The cytological details of fertilization and the rôle played by the subterminal antheridium have been described (Kevorkian, *loc. cit.*).

APODACHLYA BRACHYNEMA var. MAJOR Tiesenhausen, Arch. f. Hydrobiol. u. Planktonk., 7 (2):297, fig. 20. 1912.

Mycelium little branched, hyphae 6–13 μ in diameter, segments 15–537 μ long; sporangia spherical, rarely elongate, 40–52 μ (long?), discharge tube large, 10–20 μ long by 6–10 μ in diameter; zoospores not observed; oöspore spherical, 25–30 μ in diameter.

On twigs, SWITZERLAND.

Differing from *Apodachlya brachynema* principally in having

of same fungus emerging from cyst; K, secondary zoospore; flagella are not shown, but are laterally inserted.

(A–B, Pringsheim, 1860; C, I–K, Coker, 1923; D, Coker and Leitner, 1938; E, Zopf, 1888; F, Indoh, 1939)

longer sporangia and larger hyphae. As Coker (1923) suggests, this is probably only a form rather than a variety.

APODACHLYA MINIMA Coker and Leitner

J. Elisha Mitchell Sci. Soc., 54:313, pl. 39. 1938

(Figure 52 D, p. 566)

"Mycelium flaccid and flocculent, reaching a diameter of 2.5-3 cm. on hemp seed; main hyphae slender and segmented, branching from any point on the segment, mainly from the middle; protoplasm thin except in the oögonial branches, with small round refractive bodies present; segments $3.4-8.5 \times 47.6-170 \mu$ on hemp seed, but $6-12.2 \times 44-250 \mu$ on 2 % corn meal agar, becoming shorter at the tips. Sporangia unknown [Various experiments to produce them were unsuccessful.] Oögonia numerous, borne on the tips of short, moniliform, often recurved, lateral branches, mainly spherical, occasionally short-pyriform or oval or club-shaped or dumbbell-shaped, $12-16 \mu$ thick; wall unpitted, smooth, about 0.45μ thick. Egg single, completely filling the oogonium, excentric, the cytoplasm rounded up into a hyaline ball closely appressed to the smaller hyaline oil droplet. Antheridium originating from the sub-oogonial cell as a lateral branch which grows out and applies itself to the oogonial wall, variable in shape, usually becoming completely empty before the maturation of the egg" (Coker and Leitner, *loc. cit.*).

In a stream slightly contaminated with sewage, substratum (?),
UNITED STATES.

APODACHLYA PYRIFERA Zopf

Nova Acta Acad. Leop.-Carol., 52:367, pl. 21, figs. 1-21. 1888

(Figure 52 E, p. 566)

Leptomitus piriferus Zopf, in Schenk, Handbuch d. Bot. . . . , 4:299. 1890.

Mycelium extensive, matted, sympodially branched, the segments long or short, somewhat clavate distally, contents with one or two cellulose bodies in each segment, especially near the constrictions; sporangia terminal, single or in pairs, broadly obpyriform, citriform, fusiform, ovoid, or ellipsoidal, $12-24 \mu$ long by $12-20 \mu$ in diameter, papilla mostly terminal or somewhat lateral, with or without a short

discharge tube; primary zoospores from six to twenty, encysting at the orifice or swimming directly away, laterally biflagellate (secondary?) spores; oögonium spherical, generally terminal, or lateral on a short segment near a constriction, rarely intercalary, the antheridium suboögonial or lateral; oöspore spherical, filling the oögonium, with a thick smooth double wall, contents with a large oil globule, germination not observed.

On decaying Characeae, Zopf (*loc. cit.*), twigs, Höhnk (1935:218), substratum (?), Richter (1937), Cejp (1932b:1, pl. 1, figs. 6-9, pl. 2, figs. 4-6), GERMANY; twigs, H. E. Petersen (1909:388; 1910:526), Lund (1934:33), DENMARK; Thaxter (1896b:325), birch twigs, Sparrow (1933c:532), UNITED STATES; in soil, Wolf (1939:384), MEXICO.

The species name was spelled "*piriferus*" by Zopf in 1890 and "*pyrifera*" in 1888.

APODACHLYA PYRIFERA var. MACROSPORANGIA Tiesenhausen, Arch. f. Hydrobiol. u. Planktonk., 7(2):295, fig. 19 a-c. 1912.

Mycelium sparingly branched, hyphae 5-15 μ in diameter, segments 70-430 μ long, mostly over 100 μ long; sporangia generally single, terminal or on short lateral branches, pyriform or ellipsoidal, 35-63 μ long by 14-36 μ in diameter, with a short apical or subapical discharge tube, often collapsing after discharge; zoospores from four to twenty-four, primary spores encysting at the orifice, the cysts 11 μ in diameter, secondary spores spherical, 10-11 μ in diameter; oögonium spherical, 27-31.5 μ in diameter, borne at the tip of a short, two-linked lateral branch arising from the middle of a segment, the antheridium being a lateral link of the same hypha or apparently arising laterally from the same main axis; oöspore spherical, filling the oögonium, 25-33 μ in diameter, with a smooth thick colorless wall and two or more globules, germination not observed.

On twigs of *Picea excelsa*, Tiesenhausen (*loc. cit.*), SWITZERLAND; *Fraxinus* twigs, Sparrow (1932b:295), UNITED STATES; twigs, Lund (1934:33), DENMARK.

Although the variety so far as now known differs primarily in the larger size of the sporangia a more careful study of the sex organs may reveal other features of divergence.

APODACHLYA SERIATA Lund

Kgl. Danske Vidensk. Selsk. Skrift., Naturv. Math., Afd. IX, 6(1):34, fig. 14.
1934

"Hyphae branched, constricted into segments, which are $42.5 - 100 \times 5-10 \mu$, mostly $70-80 \times 5-8 \mu$. Sporangia pyriform, oval, or subcylindrical $35-97 \times 15-25 \mu$, generally $50-60 \times 20 \mu$, terminal on main hyphae, more rarely on lateral branches, or in rows up to four. Zoospores $10-12 \mu$ in diameter, about 26 in a sporangium; escaping through a short apical exit tube, encysting in a hollow sphere at the mouth of the sporangium. Resting spores (oogonia?) spherical, $27-32.5 \mu$ in diameter, generally borne on short side branches, composed of one to few short segments. 1 oospore (?). Antheridia possibly present" (Lund, *loc. cit.*).

On twigs of *Alnus*, DENMARK.

Characterized by long sporangia, which are often in basipetal series.

APODACHLYA PUNCTATA Minden

Kryptogamenfl. Mark Brandenburg, 5:586, fig. 15 b-d (p. 580). 1912
(1915)

(Figure 52 G-H, p. 566)

Mycelium like that of *Apodachlya pyrifera*, forming a whitish turf; sporangia spherical, subspherical, ovoid to pyriform, terminal or sympodially arranged, numerous, discharge tube usually lateral or even basal; zoospores ordinarily swimming directly away, rarely encysting at the orifice; oögonium either terminal on the main axis or on a short linklike lateral branch, antheridium basal; oöspore nearly filling the oögonium, thick-walled, golden, the wall minutely and distinctly punctate, germination not observed.

On twigs, Minden (*loc. cit.*), Höhnk (1935:218), GERMANY; twigs of *Fraxinus*, Sparrow (1933c:532), UNITED STATES.

Certain investigators (Coker, 1923:174; Coker and Leitner, 1938:313) consider the punctations of the egg to be due to the arrangement of oil globules, but in this they are mistaken. Photomicrographs of plasmolyzed oöspores show unquestionably that the wall is punctate.

APODACHLYELLA INDOH

Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:45-46. 1939

(Figure 52 F, p. 566)

"Mycelium filamentous, branched, segmented by numerous constrictions, without basal body. Hyphal segments cylindrical with cellulose grains. Hyphal membrane stainable faintly blue with zinc chloride-iodine.

"Zoosporangium not observed.

"Oogonia multisporous. Oospores without periplasmic membrane. Antheridia with several antheridial cells. Fertilization by a tube from each cell.

"Other characters as in *Apodachlya*.

"Single species" (Indoh, *loc. cit.*).

Saprophytic in fresh water or soil.

See the remarks in the introduction to the Leptomitales (p. 548).

APODACHLYELLA COMPLETA (Humphrey) Indoh

Science Rep. Tokyo Bunrika Daigaku, Sect. B, 4:46, pl. 7, figs. 1-11. 1939

Apodachlya (?) *completa* Humphrey, Trans. Amer. Phil. Soc., 17:137, pl. 20, figs. 119-121. 1893.

"Mycelium slender, filamentous, irregularly branched. Basal segments of hyphae long, cylindrical, 9 to 12 μ in diam., 130 to 200 μ in length; upper segments rather short, 2.5 to 6 μ in diam., 40 to 100 μ in length. Hyphal membrane smooth, hyaline.

"Zoosporangium unknown.

"Oogonia single, terminal, spherical, 23 to 48 μ in diam., rarely pyriform to broad cylindrical, containing 2 to 12 (usually 4 to 7) oospores; membrane thin, smooth, hyaline. Oospores spherical to subspherical, 16 to 24 μ in diam., with a large eccentric oil drop; membrane 1.5 to 1.8 μ in thickness, punctated when matured. Antheridia terminal, single or from 2 to 3 segmented filamentous antheridial branches arising from segment just below oogonia; long, cylindrical, curved, containing 4 to 10 antheridial cells. Antheridial cells spherical, hyaline, smooth, 4.4 to 4.9 μ in diam., arranged in a single row" (Indoh, *loc. cit.*).

In fresh water and soil on flies and hemp seeds used as bait. Humphrey (*loc. cit.*), UNITED STATES; Indoh (*loc. cit.*), JAPAN.

RHIPIDIACEAE

Thallus always more or less well differentiated into a basal cell, holdfasts, and jointed hyphal branches on which are borne well-defined pedicellate reproductive organs; zoosporangia smooth- or spiny-walled; zoospores laterally biflagellate, sometimes containing prominent refractive globules; antheridium single, cut off from its concomitant branch by a cross wall, forming a conspicuous fertilization tube; oögonium forming a single oöosphere which is differentiated into oöplasm and periplasm; oöspore with a smooth endospore wall surrounded either by a thick undulate or reticulate exospore wall or a cellular layer, germination not observed.

Primarily saprophytic on submerged twigs and fleshy fruits.

KEY TO THE GENERA OF THE RHIPIDIACEAE

Basal cell usually giving rise to hyphal branches bearing the reproductive organs; oöspores formed (except in *Rhipidium parthenosporum*)

Basal cell slender, usually poorly defined; sporangia smooth-walled; oöspore with undulate outer wall SAPROMYCES, p. 572

Basal cell usually stout and well defined; sporangia smooth-walled or spiny or both; oöspore with reticulate or cellular outer wall

Oöspore wall cellular; sporangia smooth and spiny-walled

ARAIOSPORA, p. 576

Oöspore wall reticulate; sporangia smooth-walled RHIPIDIUM, p. 581

Basal cell never giving rise to hyphal branches, the reproductive organs arising directly from it; parthenospores formed

MINDENIELLA, p. 588

SAPROMYCES K. FRITSCH

Oesterr. botan. Zeitschr., 43:420. 1893

(Figure 53 A-B, p. 578)

Naegelia Reinsch, Jahrb. wiss. Bot., 11:298. 1878. Non Rabenhorst, 1844; Lindley, 1845; Moritz, 1846; Regel, 1848.

Naegeliella Schroeter, in Engler and Prantl, Natürlichen Pflanzenfam., 1 (1):103. 1893. Non Correns, 1892.

Thallus differentiated into a poorly defined slender or somewhat distorted epibiotic basal cell and, arising from this, a few repeatedly

umbellately branched segmented and constricted cylindrical filaments on which are borne the reproductive organs, segments delimited by pseudosepta, the whole anchored to the substratum by a complex of endobiotic branched holdfasts; zoosporangia smooth-walled, either formed in whorls or umbels at the tips of the segments, from which they are separated by septate constrictions, or appearing lateral; zoospores somewhat reniform, laterally biflagellate, emerging upon the deliquescence of an apical papilla, often surrounded by a more or less evanescent vesicle; antheridium either diclinous or androgynous, borne at the tip of a long or short distal prolongation of the segments, apically applied, with a conspicuous fertilization tube; oögonia monandrous, spherical or pyriform, borne in whorls or umbels or on short constricted segments, the contents at maturity differentiated into oöplasm and periplasm; oöspore borne singly and loosely in the oögonium, wall thick, rough, germination not observed.

The two known species are saprophytic on decaying plant materials, especially twigs, in cooler pure waters.

Sapromyces differs from *Araiopora* in the less pronounced, more slender basal cell, in forming only smooth sporangia, and in the fact that the oöspore lacks a cellular envelope of periplasmic origin.

KEY TO THE SPECIES OF SAPROMYCES

- | | |
|------------------------------|-------------------------------|
| Antheridia diclinous | <i>S. elongatus</i> , p. 573 |
| Antheridia androgynous | <i>S. androgynus</i> , p. 575 |

SAPROMYCES ELONGATUS (Cornu) Coker

N. A. Flora, 2(1):62. 1937

(Figure 53 B, p. 578)

Rhipidium elongatum Cornu, Ann. Sci. Nat. Bot., V, 15:15. 1872.

Naegelia sp. "I" (and "II") Reinsch, Jahrb. wiss. Bot., 11:298, pl. 15, figs. 1-6. 1878.

Naegeliella Reinschii Schroeter, in Engler and Prantl, Naturlichen Pflanzenfam., 1(1):103. 1893.

Sapromyces Reinschii (Schroeter) K. Fritsch, Oesterr. botan. Zeitschr., 43:420. 1893.

Sapromyces dubius K. Fritsch, op. cit., p. 421. 1893.

Basal cell slender or somewhat distorted, 300-1200 μ long, including the branched holdfasts, by 15-30 μ in diameter, the apical cylind-

drical or narrowly clavate secondary axes more slender, constricted and septate at their point of origin, 8–15 μ in diameter and up to 620 μ in length, giving rise distally to from one to several successively narrower segments which may further branch at their apices; sporangia pedicellate, borne singly or in whorls of from two to six at the tips of the branches or at the constrictions, subcylindrical, subclavate, ovoid or ellipsoidal, 35–200 μ long by 10–30 μ in diameter; zoospores reniform, laterally biflagellate; antheridium swollen and irregularly clavate, appressed along its whole length or only by its apex to the upper part of the oögonium, borne on a slender often tortuous branched or unbranched long hypha of diclinous origin; oögonium spherical, subspherical, or pyriform, 32–63 μ high by 26–40 μ in diameter, pedicellate, borne terminally or laterally, the outer wall with age often exhibiting a brownish transversely disposed incrystation; oospore not filling the oögonium, spherical, 20–34 μ in diameter, yellowish to brownish, the thick wall with a slightly uneven outer surface, germination not observed.

On decaying stems of *Viscum*, Reinsch (1875, 1878), substratum (?) (coll. Claussen), Minden (1915:591), pine twigs, Minden (*op. cit.*, p. 590, fig. 11; 1916:pl. 7, fig. 73), apple, twigs, and cones of *Picea*, Cejp (1932c; 1936:370, text fig. D, pl. 10), Richter (1937), GERMANY; cones and twigs of *Pinus sp.*, Thaxter (1894:49, pl. 5), substratum (?) (coll. Couch), Coker (1923:176, pl. 60) (sterile), twigs of *Pseudotsuga mucronata*, Graff (1928:170), twigs of *Chamaecyparis* (coll. P. N. Jordan), Sparrow (1932b), twigs, Sparrow (*op. cit.*, p. 294, pl. 7 J), Kevorkian (1935:279), Bishop (1940:505, figs. 1–6), Matthews (1935) (sterile), UNITED STATES; twigs of *Picea excelsa*, Tiesenhausen (1912:298, figs. 21–22), SWITZERLAND; twigs of fir and spruce fir, H. E. Petersen (1910:527), apples, twigs, Lund (1934:35, fig. 15), DENMARK; Moore (1908–1909:234, figs. 23–24), CANADA; twigs of *Quercus* (coll. Barnes), Sparrow (1936a), Sparrow (1936a:460, pl. 20, fig. 11), Gwynne-Vaughan and Barnes (1937:fig. 42), ENGLAND; rose fruits and apples, Crooks (1937:216, pl. 10, fig. 4), AUSTRALIA; twigs of *Pinus*, Apinis (1930:233), LATVIA.

It is difficult to decide whether or not Reinsch's *Naegelia sp. "II,"* earlier (1875) called *Hypomycetarum*, n. gen., belongs here, but, as Minden suggests, it may be a depauperate form of *Sapromyces*.

elongatus. Since no sex organs were found in Reinsch's material, his fungus may have been the less common *S. androgynus*. This is true also of Couch's and Miss Matthews' records.

Coker and Matthews (1937:62) adopted the binomial *Sapromyces elongatus* (Cornu) Coker for this species. There is much to be said for the change, since the oöspore described by Cornu for his *Rhipidium elongatum* possessed an undulate wall. Two things, however, might be noted against the adoption of Cornu's name: (a) the absence in this species of a well-developed basal cell, the presence of which in Cornu's fungus is implied by his placing it in *Rhipidium*, (b) the lack of a figure by Cornu and his identification of the figures of Reinsch with those of his own *R. interruptum* (not *R. elongatum*). The facts do not seem to be conclusive for either name.

SAPROMYCES ANDROGYNUS Thaxter

Bot. Gaz., 21:329, pl. 22, figs. 16-19. 1896

(Figure 53 A, p. 578)

Basal cell slender, 115-247 μ long by 16-23 μ in diameter, hold-fasts few, the apical cylindrical or narrowly clavate secondary axes constricted and septate at their point of origin, about 8-16 μ in diameter, up to 180 μ long, whole plant 500-2600 μ long; sporangia pedicellate, borne singly or in whorls, subcylindrical, ovoid, or ellipsoidal, 49-109 μ long by 16-30 μ in diameter; zoospores laterally biflagellate; antheridium androgynous, applied at the apex of the oögonium, consisting of a distally swollen and irregularly clavate slender unbranched sometimes twisted segment which arises laterally just beneath the oögonium; oögonium terminal or lateral, pedicellate, spherical or broadly pyriform, colorless and smooth or with a dark scaly wall, 35-50 \times 27-30 μ ; oöspore spherical, 20-26 μ in diameter, with a thick colorless or faintly golden wall raised in a series of low uneven prominences, germination not observed.

A species of infrequent occurrence, forming dense pustules often unmixed with other Phycomycetes. On submerged sticks, Thaxter (*loc. cit.*), *Fraxinus* and other twigs, Sparrow (1932b:295, pl. 7, figs. B, I), twigs, Kevorkian (1935:279), UNITED STATES; cones and twigs of *Picea*, Cejp (1936: text figs. A-C, pl. 11), GERMANY; Weston (1938:246), NEWFOUNDLAND; Weston (*loc. cit.*), PANAMA.

ARAIOSPORA THAXTER

Bot. Gaz., 21:326. 1896

(Figure 53 C-H, p. 578)

Rhipidium Cornu, pro parte, Bull. Soc. Bot. France, 18:59. 1871.

Thallus differentiated into a well-defined epibiotic basal cell and, arising from this, numerous repeatedly umbellately branched more or less segmented and constricted cylindrical filaments on which are borne the reproductive organs, the whole anchored to the substratum by a complex of endobiotic branched holdfasts; zoosporangia formed in whorls or umbels at the tips of the segments, from which they are separated by a constriction, wall smooth or spiny; zoospores reniform, laterally biflagellate, contents finely granular, fully formed within the sporangium, emerging upon the deliquescence of an apical papilla, often surrounded by a quickly evanescent vesicle; antheridium borne at the tip of a branched or unbranched specialized segment; oögonia spherical, monandrous, borne in whorls or umbels on short lateral constricted segments, the contents at maturity differentiated into oöplasm and periplasm; oöspore borne singly in the oögonium, thick-walled, with a cellular envelope of periplasmic origin which fills the oögonium or lies loosely in it, contents granular, with a large oil globule, germination not observed.

The species are all saprophytes on plant materials, particularly floating twigs, and occur most commonly in late spring or early summer.

Araiospora differs from *Sapromyces* and *Rhipidium* not only in the curious production of spiny- and smooth-walled sporangia (Fig. 53 E-F, H) but also in the formation of a cellular envelope around the oöspore. King (1903) has concluded after a morphological and cytological study of *A. pulchra* that it shows definite affinities with the Peronosporales and stands between *Pythium* and the Saprolegniaceae. Kevorkian (1934) has stated that in *A. streptandra* the fertilization tube is of antheridial origin rather than formed by the oöplasm as King asserted (see also under "Cytology," p. 559).

Because of their symmetrical arborescent habit and exquisitely reticulated often golden oöspores these apparently rare fungi are one of the most exciting "finds" among the water molds, and their

delicate beauty never fails to elicit the admiration of the collector fortunate enough to find them.

KEY TO THE SPECIES OF ARAIOSPORA

Spiny sporangia bearing numerous long slender spines either apically or over entire surface

Oöspore not filling the oögonium, antheridium diclinous

A. spinosa, p. 577

Oöspore filling the oögonium, antheridium monoclinous

Antheridial hypha often branched, not twisted around the base

of the oögonium *A. pulchra*, p. 579

Antheridial hypha unbranched, twisted around the base of

the oögonium *A. streptandra*, p. 580

Spiny sporangia bearing a crown of from four to six short or slightly

curved digitate apical spines *A. coronata*, p. 581

ARAIOSPORA SPINOSA (Cornu) Thaxter

Bot. Gaz., 21:326. 1896

(Figure 53 F, p. 578)

Rhipidium spinosum Cornu, Bull. Soc. Bot. France, 18:59. 1871.

Basal cell broadly cylindrical, with rounded apex, in large plants up to 800 μ long by 160 μ in diameter, thick-walled, primary axes 780 μ long by 76–96 μ in diameter, coarse, umbellate, unbranched, or giving rise distally to secondary umbels, constricted and segmented only at the place of origin or beneath the reproductive organs, rarely along the filaments; sporangia usually borne in clusters or whorls of from two to eight at the tips of the branches (rarely singly), occasionally directly on the basal cell, smooth sporangia more or less narrowly ellipsoidal, 90–150 μ long by 45–60 μ broad, spiny type ovoid or broadly ellipsoidal, 100–150 μ long by 40–80 μ broad, with an apical crown of solid rigid straight or recurved spines 60–70 μ long by 9 μ broad, of variable number, often occurring in two whorls (the outer having up to eight spines, the inner up to four) around the discharge papilla; zoospores reniform, the two flagella attached in a lateral fold, contents granular; antheridium relatively large, curved-cylindrical, appressed to the oögonium along its whole length, borne at the tip of a long slender often twisted and encircling branch usually

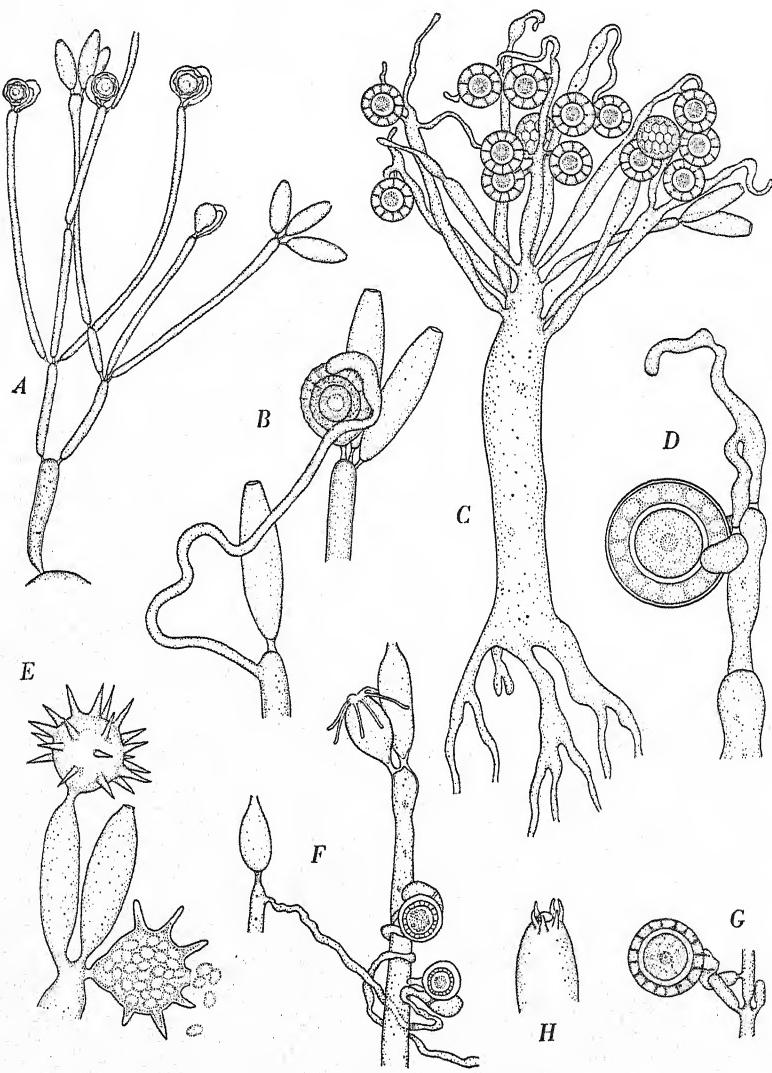


FIG. 53. Rhipidiaceae

A. Sapromyces androgynus Thaxter ($\times 75$), habit of plant showing sporangia and sex organs. *B. Sapromyces elongatus* (Cornu) Coker ($\times 250$), dioecious sex organs and discharged sporangia. *C-E. Araiospora pulchra* Thaxter: *C*, plant bearing sex organs and discharged smooth-walled

of diclinous origin; oögonia clustered on short segments, spherical, with a smooth brownish wall; oöspore spherical, not filling the oögonium, with a thick cellular wall, germination not observed.

On twigs, *Cornu* (*loc. cit.*), FRANCE; twigs of *Quercus*, *Alnus*, rhizomes of water lily, Minden (1902:822; 1915:593, fig. 10 [p. 590]; 1916:151, pl. 1, figs. 1-8), GERMANY.

Aside from a brief statement by Cornu that certain sporangia possessed long straight or recurved spines, our whole knowledge of this species is due to the investigations of Minden. He not only studied the plant in its natural habitat but obtained pure bacteria-free cultures on plum gelatin decoction and liquid media. This has never been successfully achieved by the few subsequent observers of species of *Araiospora*.

Minden's descriptions and figures indicate that the inner oöspore wall is very thin and appears to form the inner face of the peripheral cells.

ARAIOSPORA PULCHRA Thaxter

Bot. Gaz., 21:328, pl. 23, figs. 20-25. 1896

(Figure 53 C-E)

Basal cell predominantly large, thick-walled, 800-1500 μ long by 25-50 μ in diameter, the apex subcylindrical or subconical, bearing numerous secondary axes 275-2750 μ long which are constricted and septate at the base and repeatedly and umbellately branched distally, the segments of the branches subcylindrical and becoming successively longer and more slender, holdfasts coarse, much branched; sporangia borne in whorls or umbels, smooth sporangia subcylindrical or broadly clavate, 120-175 \times 30-35 μ , spiny sporangia broadly ovoid to pyriform, 60-70 \times 45-48 μ , the spines coarse, 10-35 μ long, radiating from the whole surface of the sporangium; zoospores emerging

sporangia (\times 75); D, detail of sex organs (\times 250); E, spiny and smooth-walled zoosporangia, one sporangium in process of discharging its zoospores. F. *Araiospora spinosa* (Cornu) Thaxter, spiny and smooth sporangia and sex organs. G. *Araiospora streptandra* Kevorkian (\times 175), sex organs. H. *Araiospora coronata* Linder (\times 250), tip of sporangium showing crown of spines around discharge orifice.

(A-D, Sparrow, 1932b; E, Thaxter, 1896b; F, Minden, 1916; G, Kevorkian, 1934; H, Linder, 1926)

singly or in a mass; antheridium terminal, monoclinous, somewhat clavate, applied at the base of the oögonium, borne on a recurved branched or unbranched segment; oögonia borne like the sporangia, pedicellate, terminal, spherical, smooth-walled, $30-60 \mu$ in diameter; oöspore spherical, thick-walled, golden, $35-45 \mu$ in diameter, the contents with a single globule, peripheral cells polygonal, about $7 \times 10 \mu$, the whole completely filling the oögonium, germination not observed.

On twigs, particularly *Fraxinus*, Thaxter (F.) (*loc. cit.*), King (1903:211, pl. 11-15), Sparrow (S., B. M.) (1932b:296, pl. 8 f-g), UNITED STATES.

The species occurs in association with *Sapromyces* and *Monoblepharis* in late spring. It may form pustules, but more commonly single plants occur. The cytology of the species has been investigated by King (see p. 559).

ARAIOSPORA STREPTANDRA Kevorkian

Mycologia, 26:151. 1934

(Figure 53 G, p. 578)

"Large sub-cylindrical basal cell with many branches arising from the sub-conical apex. Branches separated by constrictions and repeatedly and umbellately branched, each successive segment becoming more elongate and slender than its predecessor. Sporangia borne singly or in whorls of two to six of two types (1) sub-cylindric or broadly clavate and smooth, $79-111 \times 29-49 \mu$, (2) oval or pyriform and spiny, $60-78 \times 46-63 \mu$. Spines numerous, 15 to 30μ in length, elongate conical in shape. Antheridia borne singly on short, stout lateral branches, usually originating near the distal ends of the segments, twisted about the base of the oögonia, irregular in outline. Oögonia spherical, $52-68 \mu$ (av. $60-64 \mu$), arising similarly to and usually near the antheridia. Oöspore spherical, 39 to 46μ (av. 44 to 46μ), surrounded by a single layer of hexagonal-appearing peripheral cells derived from the periplasm. Germination of the oöspore not observed" (Kevorkian, *loc. cit.*).

On submerged twigs of *Prunus* and *Salix* (F.), UNITED STATES.

Distinguished from *Araiospora pulchra*, which it most closely resembles, by the twisted unbranched irregular antheridium, which arises as a short lateral branch near the tip of a segment.

ARAIOSPORA CORONATA Linder

Mycologia, 18:176, pl. 21, figs. 1-14. 1926
(Figure 53 H, p. 578)

"Basal cell subcylindrical, 826-846 X 45-48 μ , with well developed branched rhizoidal system at the base, and giving rise to few or many sporangiophores at the rounded apex. Sporangiophores with constrictions and repeatedly and umbellately branched, the segments successively more elongate and slender. Zoosporangia elongate-elliptical to subcylindrical, occurring singly or in whorls of two to six, terminating the branches or at the distal ends of the segments which make up the branches. Sporangia of two types: simple sporangia smooth, 63-85 X 11.5-16.2 μ ; spinose sporangia with 4-6 short (7-9 μ), straight or slightly curved finger-like spines in a circle around the apical papilla of discharge, 68-130 X 12-26 μ . The entire plant 5 mm. in length. Oospores not observed" (Linder, loc. cit.).

On submerged fruit and twigs (F., L. 258), SOUTH AMERICA (BRITISH GUIANA).

Although no sexual organs were found in this species, the crown of from four to six short straight or slightly curved spines on the spiny sporangia distinguishes it from *Araiopora pulchra*, *A. streptandra*, and *A. spinosa*.

RHIPIDIUM CORNU

Bull. Soc. Bot. France, 18:58. 1871. Non *Rhipidium* Bernhardi, in Schrader, Journ. für die Botanik, 2:127. 1800 (1801); non *Rhipidium* Wallroth, Flora cryptogamica Germaniae, 2:742. 1833

(Figure 54, p. 582)

Thallus differentiated into a well-defined more or less epibiotic basal cell and hyphal branches, basal cell consisting of a proximal cylindrical main axis surmounted by an expanded peltate, lobed, contorted, or branched thick-walled distal platform (the axis or the platform sometimes lacking); reproductive organs pedicellate on constricted septa, arising singly or in umbellate clusters from branches of the axis, or, more commonly, directly from the edges of the platform, or terminally on long upright cylindrical branches which are constricted and pseudoseptate at their point of origin on the edge of

the platform, or appearing lateral by sympodial branching of the supporting filaments, the whole thallus anchored in the substratum by a branched system of filamentous holdfasts; zoosporangia borne

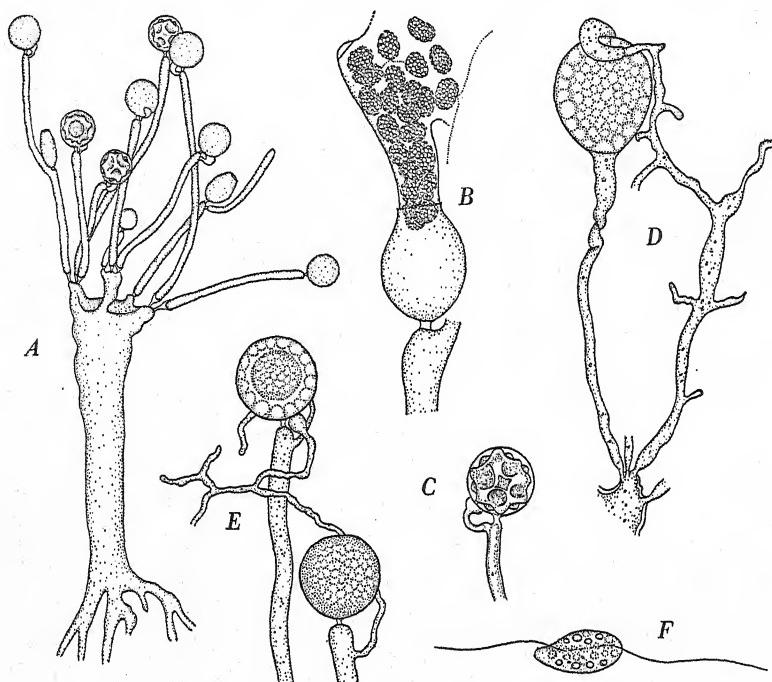


FIG. 54. *Rhipidium*

A-C. Rhipidium americanum Thaxter: *A*, habit of plant with zoosporangia and sex organs ($\times 90$); *B*, discharge of zoospores; vesicle surrounding emerged spores has just split; *C*, sex organs ($\times 185$), showing androgynous antheridium and oöspore in surface view. *D. Rhipidium Thaxteri* Minden, habit of sex organs, showing oogonium with apically applied antheridium. *E. Rhipidium interruptum* Cornu, habit of diclinous sex organs. *F. Rhipidium* sp., zoospore (freehand drawing).

(*A, C*, Sparrow, 1932b; *B*, after Thaxter, 1896b; *D-E*, after Minden, 1916)

singly or in umbellate clusters, with a single discharge papilla; zoospores reniform, laterally biflagellate, contents with numerous coarse refractive granules, formed within the sporangium, emerging

in a cylindrical group upon the deliquescence of the apical papilla, generally surrounded by an evanescent vesicle; antheridium single, androgynous, monoclinous or diclinous; oögonia borne like the zoosporangia; oöspore borne singly and loosely in the oögonium, thick-walled, areolate or stellate, germination not observed.

The plants form white gummy pustules, primarily on twigs and rosaceous fruits.

The habit of the thallus even in a single species is extremely variable and identification of the species is impossible unless the sex organs are present. One species (*Rhipidium parthenosporum*) forms thin-walled parthenospores rather than oöspores.

Lütjeharms (1937) has presented the arguments for conserving "*Rhipidium*" against several earlier homonyms.

KEY TO THE SPECIES OF RHIPIDIUM

Antheridium present; oöspore stellate, not filling the oögonium

Antheridium diclinous, monoecious, or dioecious

Antheridium applied at the base of the oögonium

R. interruptum, p. 583

Antheridium applied at the apex of the oögonium *R. Thaxteri*, p. 586

Antheridium androgynous *R. americanum*, p. 587

Antheridium lacking, parthenospore smooth-contoured, filling the oögonium *R. parthenosporum*, p. 588

RHIPIDIUM INTERRUPTUM CORNU

Bull. Soc. Bot. France, 18:58. 1871; van Tieghem, Traité de Botanique, p. 1024, fig. 617. 1884. Paris

(Figure 54 E)

Rhipidium continuum Cornu, Bull. Soc. Bot. France, 18:58. 1871.

Rhipidium europaeum Minden, Kryptogamenfl. Mark Brandenburg, 5:597, fig. 9 (p. 590). 1912 (1915); Falck, Mykolog. Untersuch. Berichte, 2 (2):187, figs. 3, 5-14, pl. 2, figs. 12-19. 1916.

Rhipidium europaeum var. *interruptum* Minden, in Falck, Mykolog. Untersuch. Berichte, 2:172. 1916.

Basal cell with or without a cylindrical axis, 400-900 μ long by 30-90 μ in diameter, the platform extremely variable in size and shape, either swollen, contorted, gnarled, divided into broad branch-

like lobes or appressed and peltate, up to 800 μ broad, the lobes attaining a breadth of 150 μ or more, the wall variable, often 20 μ thick, sometimes roughened; cylindrical branches numerous, generally arising from the apices of the lobes of the platform, constricted and pseudoseptate at the base, more or less constricted and often pseudoseptate along their length, 7–14 μ in diameter by 100–500 μ long, rarely branching, holdfasts extensive, branched; sporangia generally single, terminal, borne on short subspherical segments or sympodially arranged on long cylindrical branches, ovoid to ellipsoidal, sometimes nearly spherical, 40–70 μ long by 25–47 μ in diameter, papilla apical, wall smooth, very thin and collapsing after discharge or stout; zoospores reniform, 12–13 μ , biflagellate, contents with numerous refractive granules; antheridium small, 19 μ long by 15 μ wide, somewhat clavate or spherical and appressed distally to the lower part of the oögonium, borne at the tip of a long slender branched or unbranched often tortuous hypha of diclinous, monoecious, or dioecious origin; oögonia borne like the sporangia on the same plant, pedicellate, spherical or pyriform, 40–60 μ in diameter, wall stout, smooth, colorless; oöspore spherical or ellipsoidal, 40–50 μ in diameter, colorless or slightly golden, not filling the oögonium, the inner wall thin, smooth, the outer very thick (up to 17 μ) and raised in an irregular series of broad ridges and protuberances, stellate in section view, germination not observed.

Forming dense pustules, sometimes mats, on fruits and twigs. On twigs, Cornu (*loc. cit.*), FRANCE; fruits and twigs, Minden (*loc. cit.*), Laibach (1927:599), Behrens (1931:745, figs. 1–33), plum twigs, Höhnk (1935:218), GERMANY; twigs of alder, birch, fir, H. E. Petersen (1909:389; 1910:526, fig. 4 a, e), twigs, apples, Lund (1934:36, fig. 16), DENMARK; fruits, Boedjin (1923:fig. 1), HOLLAND; fruits, Kanouse (1926:113, pl. 1, fig. 2; 1927:341, pl. 48, figs. 27–33, 39), UNITED STATES; apples, Valkanov (1931a:366), BULGARIA; rose fruits, Forbes (1935a:234, fig. 1; 1935b:3), fruits, twigs of *Fraxinus*, Sparrow (1936a:459, pl. 20, figs. 6, 10), ENGLAND.

The cytology of the species (see p. 556) has been studied by Behrens (*loc. cit.*).

Probably synonymous with this species is *Rhipidium compactum* Matthews (1936:292, pl. 25), which differs significantly from *R. interruptum* only in having the oögonia minutely papillate in many

instances. *R. compactum* is not mentioned in Coker's and Matthews' 1937 paper. Matthews' (1936) description of it follows:

Plants appearing on the substratum as small whitish pustules about 0.5-1 mm. in diameter. Individual plants composed of a main trunk, which may or may not be branched, a large number of short secondary branches on which the reproductive organs are borne, and a well developed system of large branched often lobed rhizoids, which may extend into the substratum up to a distance of about 725μ . Main trunk unbranched or with as many as 8 large branches, $60-83 \mu$ in diameter by $99-214 \mu$ long, constricted slightly at the base where the rhizoids originate. Short secondary branches $9-42 \mu$ (majority about 20μ) long, from the large trunk, constricted at their point of origin bear the sporangia and oogonia, usually singly, occasionally two, very rarely three. Sporangia 2-10 on a main branch, very variable in shape on the same plant, globose to pyriform ones $33-36 \times 42 \mu$, cylindrical ones $20-29 \times 49-70 \mu$. Zoospores (rarely produced in the laboratory) reniform, biciliate, $6.4-8 \times 11.2-12.8 \mu$, monoplanetic. Oogonia borne on same plant as sporangia and mixed with them, at times even arising from same short branch that bears a sporangium, spherical, $26-40 \mu$ in diameter, wall thin, smooth or usually with minute papillae. Oospores one to an oogonium, $29-33 \mu$ in diameter, wall at maturity sculptured and about 6.6μ thick. Antheridia one to each oogonium forming a tube to the oosphere and borne on a long antheridial stalk arising from same plant but not from branch bearing the oogonium or in some cases perhaps from a separate plant.

On huckleberry and *Amelanchier* fruits, in Mountain Lake at Mountain Lake, Giles County, Virginia, July and August 1936.

The following variety and form have been described by Miss Forbes and Miss Kanouse respectively. Variations in the species are so common, however—far more striking than any formal diagnosis can depict—that at the moment the character of the sex organs alone seems of important taxonomic value.

RHIPIDIUM EUROPAEUM (INTERRUPTUM) var. *COMPACTUM* Forbes,
Trans. Brit. Mycol. Soc., 19:234, pl. 10, fig. 11. 1935.

"Thallus of a very short, broadly cylindrical basal cell bearing a large number of broad, subdivided lobes, which spread out and around the short stalk in a compact bunch; these lobes bear the narrow branches which are rather shorter than in the normal form. Rhizoidal system relatively well developed, rhizoids stout with rounded tips. Sporangia as in the species, $50-60 \times 25-35 \mu$. Oogonia pear-shaped,

smaller than in the species, $40-45 \mu$ diameter. Oospores smaller than in the species, $28-36 \mu$ diameter. Antheridia as in the species" (Forbes, *loc. cit.*).

Substratum (?), ENGLAND.

This variety is probably based on the peltate form commonly found in both this species and *Rhipidium americanum*.

RHIPIDIUM INTERRUPTUM f. ATTENUATA (Kanouse) Coker, N. A. Flora, 2(1):67. 1937.

Rhipidium europaeum f. *attenuata* Kanouse, Amer. J. Bot., 14:342, pl. 48, figs. 27-33. 1927.

"Vegetative plant very slender, attached by long, slender penetrating rhizoids. Basal portion very long and narrowly subcylindrical, simple or sometimes once forked, $2000-3200 \times 20-50 \mu$, wall relatively thick, $7-10 \mu$, protoplasm hyaline, including numerous oil globules upward. Branches scanty, arising from the apex of the main portion, differentiated at point of origin by pedicel-like constrictions which are provided with perforated cellulose deposits, very slender and flexible, $200-500 \times 6-9 \mu$. Asexual reproduction typical" (Kanouse, *loc. cit.*).

On *Crataegus* and apple fruits, UNITED STATES.

Differing chiefly in having a slender, sometimes once-branched, basal cell.

RHIPIDIUM THAXTERI Minden

Kryptogamenfl. Mark Brandenburg, 5:600. 1912 (1915); Falck, Mykolog. Untersuch. Berichte, 2(2):188, pl. 3, figs. 22-24. 1916
(Figure 54 D, p. 582)

Basal cell as in *Rhipidium interruptum*, often monstrous and discoid, over 800μ in diameter with lobes up to 200μ broad, or occasionally more cylindrical, upright filaments constricted only at the base, $7-11 \mu$ in diameter, free-floating, holdfasts branched; sporangia borne as in the other species or in whorls, narrowly ellipsoidal, $50-55 \mu$ long by $20-35 \mu$ in diameter; zoospores as in other species; antheridium irregularly spherical, strikingly large, curved around and adnate to the oögonium at the apex, $50-70 \mu$ long by $7-11 \mu$ broad, arising from a narrow tortuous short branched dichotomous filament

produced from the basal cell, monoecious; oögonium somewhat pyriform, 45–57 μ broad by 57–62 μ long with a broad rounded top and a narrow stalklike unconstricted attenuated base, wall moderately thick, somewhat wrinkled at maturity, arising from a short somewhat spirally twisted basally constricted stalk produced from the basal cell; oöspore large, very thick walled, the outer wall sculptured as in the other species.

On fruits and twigs, occurring with *Blastocladia* and *Rhipidium interruptum*, GERMANY.

This truly remarkable species has apparently remained unobserved since Minden's time. He regarded it as a connecting link between *Rhipidium* and *Sapromyces*, its habit and oöspore resembling the former genus, its oögonia and whorled sporangia, the latter.

RHIPIDIUM AMERICANUM Thaxter

Bot. Gaz., 21:327, pl. 21, figs. 1–15. 1896

(Figure 54 A–C, p. 582)

Thallus and arrangement of reproductive organs (except the antheridia) as in *Rhipidium interruptum*, not significantly different in size; sporangia 30–90 μ long by 20–46 μ in diameter; zoospores laterally biflagellate, reniform, 10–12 μ long, contents with numerous refractive granules; antheridium broadly clavate, 11–14 μ wide, androgynous, borne on a short arched branch which arises immediately below the oögonium; oögonium 33–55 μ in diameter; oöspore 28–46 μ in diameter, the heavy wall colorless or pale golden and ornamented as in *Rhipidium interruptum*, germination not observed.

In dense gummy pustules or mats. On various vegetable materials, Thaxter (*loc. cit.*), fruits of *Crataegus*, rose, apple, Kanouse (1927:343, pl. 48, fig. 38 a–c), apples, *Crataegus*, Sparrow (1932b:297, pl. 8 a–b; 1933c:532), UNITED STATES; fruits and twigs, Minden (1915:599; 1916:188, pl. 3, fig. 21), Cejp (1932b:1, pl. 1, figs. 1–5, pl. 2, figs. 1–3), GERMANY; apples, twigs of *Alnus*, Lund (1934:37, fig. 17 a–b), DENMARK; rose fruits, Forbes (1935a:235, fig. 2; 1935b:3), twigs of *Quercus*, Sparrow (1936a:460, pl. 20, fig. 2), ENGLAND.

The record of Crooks (1937:218, pl. 10, fig. 5) from Australia is open to question, since no sex organs were found. This species

cannot be distinguished from *Rhipidium interruptum* except in the sexual stage.

RHIPIDIUM PARTHENOSPORUM Kanouse

Amer. J. Bot., 14:344, pl. 48, figs. 34-37. 1927

Basal cell slender and elongate, once or twice forked, 800-1000 μ long by 25-30 μ wide, wall smooth, colorless, 7-10 μ thick, branches very short, ellipsoid or globose, umbellate, constricted at the point of origin and beneath the reproductive organs, constrictions with cellulose deposits, holdfasts few; sporangia ellipsoidal, thin-walled, 32-60 μ long by 25-50 μ wide, borne in umbellate clusters on short branches; zoospores not observed; antheridia lacking; oögonia spherical, thin-walled, 52-54 μ in diameter, pedicellate, borne in umbellate clusters on the short branches, the contents during development differentiated into oöplasm and periplasm, the latter with strongly marked radiating periplasmic strands and appearing cellular; mature parthenospore not observed. (Modified from Kanouse.)

In dense mats or loose tufts. On apple, Kanouse (*loc. cit.*), UNITED STATES; apples, Lund (1934:38, fig. 17c), DENMARK; twigs, Sparrow (1936a:460), ENGLAND.

Sparrow (*loc. cit.*) observed that spherical smooth somewhat thick-walled bodies formed in and completely filled the oögonia. These may be the mature parthenospores.

MINDENIELLA KANOUSE

Amer. J. Bot., 14:301. 1927

(Figure 55 A-F)

Thallus consisting of a narrowly clavate occasionally cylindrical basal cell anchored to the substratum by a system of branched holdfasts; zoosporangia smooth-walled or spiny, borne on short narrow thick-walled pedicels which arise directly from the surface of the basal cell; zoospores of the secondary, biflagellate type, completely formed in the sporangium, contents bearing numerous globules, emerging through an apical pore; resting spore apogamously developed, thick-walled, entirely filling its spiny-walled container, germination not observed.

On decaying rosaceous fruits in fresh water.

Recent observations on *Mindenella* by Sparrow and Cutter (1941) have shown that the zoospores (Fig. 55 C) of this fungus are biflagellate and hence that the genus should be placed in the Leptomitales rather than in the Blastocladiiales, as it was by its discoverer.

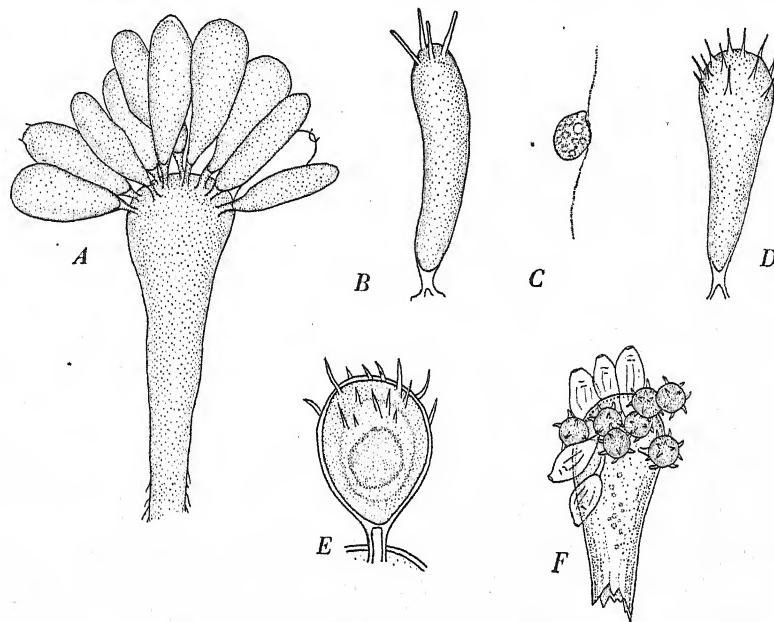


FIG. 55. *Mindenella spinospora* Kanouse

A. Tip of plant showing enlarged apex of basal cell from which pedicellate zoosporangia arise directly ($\times 280$). B. Spiny sporangium. C. Zoospore ($\times 600$). D. Another type of spiny sporangium ($\times 600$). E. Immature resting spore (?) ($\times 600$). F. Tip of plant bearing zoosporangia and resting spores.

(A-C, E, after Sparrow and Cutter, 1941; F, Kanouse, 1927)

MINDENIELLA SPINOSPORA Kanouse

Amer. J. Bot., 14:301, pl. 34. 1927

Basal cell narrowly clavate, rarely cylindrical, predominantly unbranched but occasionally divided apically into two blunt lobes, $200-850 \mu$ long by $100-200 \mu$ in greatest diameter, about $30-40 \mu$ in diameter at the base, from which emerges a system of branched

holdfasts, wall thick, occasionally with exfoliated material on its outer surface, contents coarsely granular; zoosporangia arising in most cases from the upper, expanded part of the basal cell, occasionally lower down, borne on short, narrow, thick-walled pedicels from which they are separated by a cellulose plug, predominantly narrowly and symmetrically clavate or ovate, occasionally slightly constricted in the mid-region, somewhat variable in size, 70-250 μ long by 33-75 μ in greatest diameter, smooth-walled or with 1-8 slender spines irregularly disposed around the conspicuous apical discharge papilla; zoospores of the secondary, biflagellate type, 8-15 μ long by 6-10 μ wide, contents bearing numerous small refractive globules, the spores first emerged surrounded by a delicate quickly evanescent vesicle; resting spores brownish, borne like the sporangia the outer wall of the container either wholly or in its upper part beset with numerous delicate spines 14-30 μ long, germination not observed.

Saprophytic on decaying rosaceous fruits, Kanouse (*loc. cit.*) Sparrow and Cutter (1941: figs. A-H), coll. E. A. Bessey (S.), and M. Springer (S.), UNITED STATES (MICHIGAN).

LAGENIDIALES

THE order Lagenidiales as here defined includes a group of microscopic endobiotic parasitic fungi found in fresh waters and, less often, in marine waters. Four genera of this order, *Myzocytium*, *Lagenidium*, *Resticularia*, and *Ancylistes*, together with *Achlyogeton*, were in the past included in the old order Ancystistales, primarily on the basis of their segmented thalli. Recent investigations, however, have, as in the chytrids, proved the fallibility of the grouping of fungi on similarity of body structure alone. Butler (1928), for example, pointed out that *Achlyogeton* could scarcely be allied to *Myzocytium* and *Lagenidium*, since it possessed posteriorly uniflagellate zoospores. Furthermore, the recent work of Miss Berdan (1938) shows clearly that *Ancylistes* itself, whose nonsexual reproduction had never been observed, is in fact a conidial phycomycete closely allied to the Entomophthorales. Other genera of uncertain position have from time to time been suggested as belonging in the heterogeneous Ancystistales (*Protascus*, *Lagenidiopsis*, and so on), but their inclusion has been open to question.

On the other hand, it is now evident that *Olpidiopsis*, long regarded as a chytrid, is actually allied to *Myzocytium*. Although Zopf (1884:173) pointed out the similarity of *Olpidiopsis* to *Myzocytium*, it was Scherffel (1925a) who showed the many resemblances of these two groups of fungi to each other and gave abundant evidence that *Olpidiopsis* could not be considered a chytrid. The relationship to *Lagenidium* of the little-known marine genera *Sirolpodium* and *Pontisma* was stressed by H. E. Petersen (1905:482) and has been substantiated by subsequent morphological studies (Sparrow, 1934c, 1936b). As a result of these changes the order Lagenidiales (the name proposed by Karling, 1939b:518, on the basis of Miss Berdan's work) now bears little resemblance to the Ancystistales of Fischer (1892), Schroeter (1893), and Minden (1915).

Members of the order are of infrequent occurrence and are known primarily as parasites of algae and filamentous aquatic Phycomycetes, although a few are parasitic in fresh-water microscopic animals and seaweeds. One, *Lagena* (Vanterpool and Ledingham,

1930), has been found parasitic in the roots of certain cereals and wild grasses; another, *Olpidiopsis Riccieae* (du Plessis, 1933), occurs in liverworts. A few species are probably saprophytic or attack only moribund organisms. The majority, however, are true parasites, many appearing on only a few hosts. Members of the order are alike in being endobiotic, having walls which generally give a cellulose reaction, forming zoospores with two oppositely directed flagella, and possessing a type of sexuality involving the fusion of the contents of two thalloid bodies, with the consequent production in one of a thick-walled resting spore. In the Olpidiopsidaceae and certain Lagenidiaceae the thallus is always one-celled. In other species it is one-celled or multicellular and monophagous, and in the most highly developed species it is multicellular, somewhat filamentous, hypha-like, and polyphagous.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

Infection is accomplished by the free-swimming zoospore, which comes to rest on the surface of the substratum and withdraws its flagella. In some forms it may move amoeboidly before surrounding itself with a rigid wall and producing an infection tube (Fig. 56 A-E). This needle-like structure subsequently penetrates the host wall and conveys the contents of the cyst through the wall into the interior of the substratum (Fig. 56 F-G). The development and type of thallus subsequently formed varies with the group.

In the Olpidiopsidaceae, the members of which are primarily parasitic on filamentous water molds, the thallus, unlike that of the Lagenidiaceae and possibly of the Sirolpidiaceae, is ordinarily never found attached to the tip of the penetration tube, but, as Scherffel (1925a) points out, is almost wholly monad-like and undergoes its development free in the host. Differences in the success of infection by the zoospores have been noted by Butler (1907), who concludes that they are due possibly to variations in the infective powers of the zoospores, but more likely to the age of the hyphae attacked. It has been noted by many observers that the younger parts of the vegetative system of the host are most readily penetrated, owing, perhaps, to the unmodified condition of the walls. Since the young thallus of the Olpidiopsidaceae is free in the host cell it may be carried, perhaps at first by its own action (Diehl, 1935), but more likely by

the cytoplasmic currents of the host (Diehl, *op. cit.*; McLarty, 1941a), for varying distances away from the original point of infection (Fig. 56 D-H). Often it tends to develop in the more distal regions of the

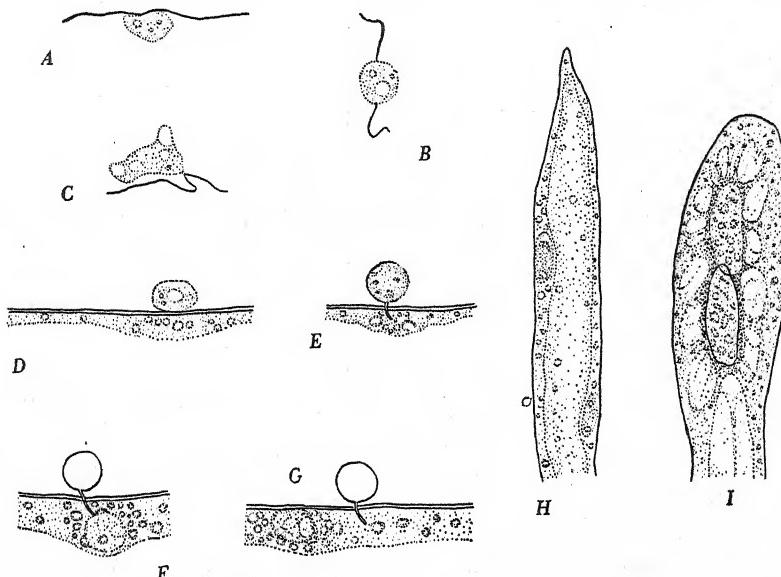


FIG. 56. *Olpidiopsis Achlyae* McLarty on *Achlya*

A. Free-swimming zoospore. B-C. Two quiescent zoospores showing changes in shape of body. D. Zoospore quiescent on outer surface of wall of host hypha, other boundary of which is not shown. E. Encysted spore, which has now produced penetration tube that has pierced host wall. F. Encysted parasite after contents have been discharged into host. G. Very young thallus of parasite being swept away (to left) from tip of penetration tube by streaming host protoplasm. H. Two young thalli of parasite suspended in peripheral cytoplasmic layer of host. I. Two more mature thalli which have assumed a central position in now distinctly swollen tip of host filament. (B-F, $\times 1730$; H-I, $\times 540$.)

(McLarty, 1941a)

hypha, though in other instances it remains intercalary. Wherever the thallus develops, a marked hypertrophy of the host occurs (Fig. 56 I). The stimulation to swell, or to produce lateral outgrowths, may possibly be due to the intake of water, since vacuoles are common, or to the accumulation of host protoplasm.

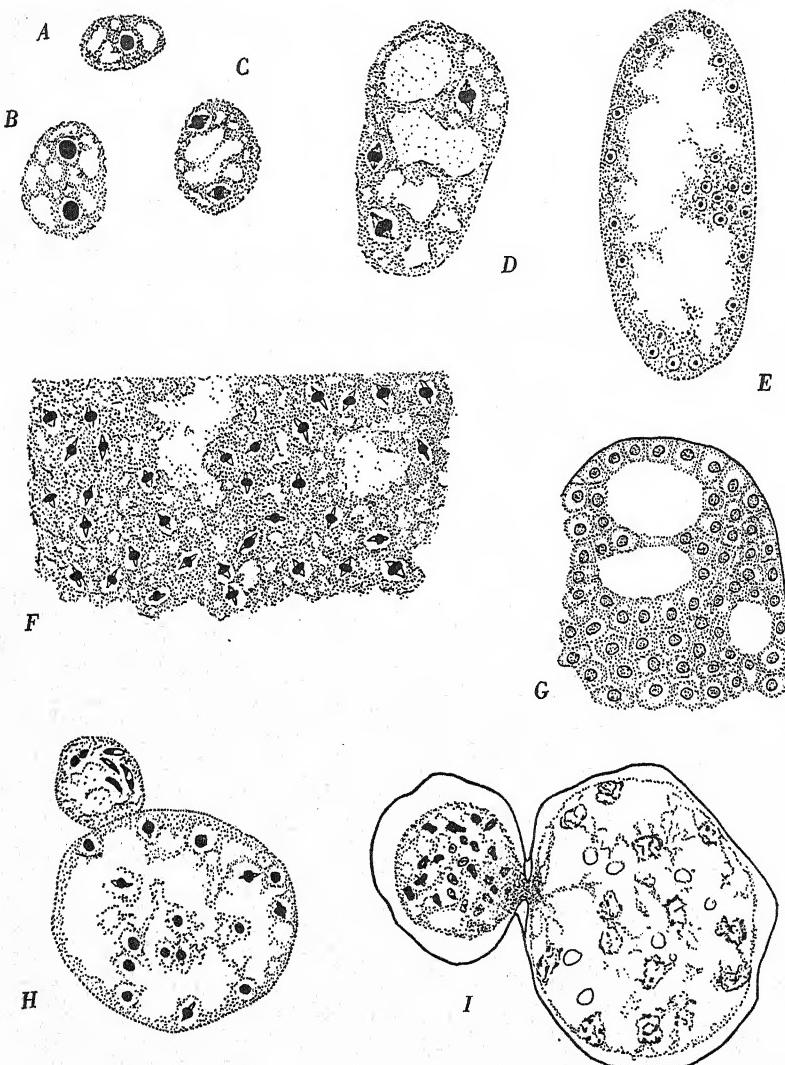


FIG. 57. Cytology of *Olpidiopsis vexans* Barrett

A. Very young uninucleate thallus soon after establishment in host hypha. B. Binucleate stage. C. Binucleated thallus with nuclei dividing, spindles intranuclear. D. Somewhat older thallus, showing vacuolate cy-

In species of *Olpidiopsis* appearing in water molds, the development and cytology of which are well known from the work of several investigators (particularly Barrett, 1912b; Diehl, 1935; McLarty, 1941b; and Shanor, 1939b, 1940), the very young thallus is uninucleate, slightly granular, and surrounded by a delicate membrane (McLarty, *op. cit.*). As it enlarges, according to Barrett, the refractive apparently fatty granules increase in number and size and a cellulose wall is secreted by the thallus, which has by now assumed a spherical or ellipsoidal shape. The contents then become more dense and are augmented by many small granules and an increased number of refractive fat bodies. The host cytoplasm at this stage forms a dense layer around the parasite, and protoplasmic streamers, between which are large vacuoles, are produced. These protoplasmic strands radiate from the region of the parasite to the peripheral cytoplasmic layer of the hypha of the host. This radiate disposition of the host contents is less extensive as development proceeds. The thallus of the parasite then becomes vacuolate, the fat bodies within it disappear, and its protoplasm assumes a densely granular texture. It may rest in this stage for several weeks, or its contents may cleave into zoospores at once.

The cytological investigations of *Olpidiopsis* by Barrett (1912b) (see also McLarty, 1941b) show that the young uninucleate vacuolated thallus (Fig. 57 A), after about doubling its original size, becomes binucleate (Fig. 57 B). The nuclei thus formed are large and have a well-defined nucleolus. Division is mitotic, the spindles being intranuclear (Fig. 57 C-D). As the rather evenly contoured thallus increases in size it is continually more vacuolate, and the nuclei are augmented in number by simultaneous divisions. In an advanced, but as yet unwalled, stage the protoplasm and nuclei line the periphery of a large irregular central vacuole (Fig. 57 E). At about this time a distinct granulation of the outside margin of the thallus is

toplasm and nuclei in division. *E*. Young sporangium, showing peripheral arrangement of cytoplasm. *F*. Portion of developing sporangium in which large vacuoles are forming and nuclei are undergoing final division. *G*. Portion of sporangium after segmentation of zoospores has occurred. *H*. Vacuolate receptive (large) and contributing (small) thalli containing irregularly distributed dividing nuclei. *I*. Connection between the two thalli established, nuclei of smaller thallus dividing, those of larger, resting.

(Barrett, 1912b)

detected, which probably marks the initial stages in wall formation. There then ensues a gradual inward growth of the protoplasm, a decrease of vacuolization with continued rapid nuclear division, and an increase in size. A well-defined wall has now been formed. After the last division of the nuclei (Fig. 57 F) the remaining vacuoles become regular in outline, and the nuclei themselves, regularly spaced in the cytoplasm, go into the resting state (Fig. 57 G). No evidences of amoeboid movement or of the fusion of thalli to form a plasmodium were observed by Barrett or McLarty.

The thallus of the *Sirolpidiaceae* (Petersen, 1905; Sparrow, 1934c, 1936b) is tubular, septate, and branched or unbranched. In *Sirolpodium* two main types of vegetative structures are formed. The first is somewhat spherical or elliptical, distinctly olpidioid, and occurs singly or in dense linearly arranged groups (Fig. 60 B, D, p. 644). These bodies are the thalli which were considered by de Bruyne (1890) to be typical of "*Olpidium*" *Bryopsidis*. At maturity each is provided with a single discharge tube, of varying length, which usually penetrates the wall of the host. The precise method of formation of such groups has not been ascertained. It has been suggested by Petersen (1905) that they have been produced from zoospores discharged inside the alga. The second type of thallus formed in *Sirolpodium* is an exceedingly interesting one. In very early stages the body of the fungus is a somewhat irregular curved cylindrical tube, often lying near the periphery of the central cavity of the host cell (Fig. 60 A). The thallus, after a period of growth, characterized mainly by elongation, becomes separated by constrictions into a linear series of spherical or cylindrical segments of varying size, each of which at maturity is disarticulated and becomes an independent, walled unit (Fig. 60 C, E, G). These fragments then for a time undergo individual growth. Each one soon loses its original orientation with respect to the parent thallus and ultimately becomes a single sporangium equipped with a discharge tube.

The thallus of *Pontisma* (Petersen, 1905; Sparrow, 1934c), though resembling to a degree that of *Sirolpodium*, is more irregularly cylindrical and usually forms short branches (Fig. 61 A, p. 646). At maturity thin cross walls are laid down which delimit irregular, constricted segments. Rarely, what appears to be a rudimentary type of fragmentation may be found. The typical mature thallus consists of a series of somewhat variously shaped connected segments.

Occasionally it may be an unsegmented cylindrical structure which curves around the periphery of the utricle of the host cell (Fig. 61 B). The contents of the thallus, though varying in aspect from time to time, generally contain during the period of vegetative activity a large number of regularly placed vacuoles. In more mature plants the protoplasm consists of a mass of closely packed refractive granules.

Each of the segments of the thallus is ultimately transformed into a sporangium having a single discharge tube (Fig. 61 E, p. 646). Tubes not oriented so as to secure egress from the host cell may ramify extensively within the substratum, frequently simulating to an astonishing degree the hyphae of filamentous Phycomycetes. Unusual powers of growth have also been observed in the discharge tubes of *Sirolopidium* (Fig. 60 F, p. 644) (Sparrow, 1934c, 1936b).

The development and morphology of the thallus of aquatic genera of the Lagenidiaceae are well known from the excellent researches of Zopf (1884) and, in recent years, of Scherffel (1925a). In both *Lagenidium* and *Myzocytium* the zoospore accomplishes infection of the host in the same manner as in the Olpidiopsidaceae. Zopf noted, however, that the cyst and the infection tube of *L. Rabenhorstii* persisted throughout the life of the thallus, whereas those of *Myzocytium* soon disintegrated. A similar situation has been found by Scherffel (*op. cit.*) in several other species of *Lagenidium*. In *L. Rabenhorstii* the minute sphere of protoplasm, once established within the alga, elongates to form a relatively thick tube. As this increases in length, irregular swellings, which originate as papilla-like or clavate protrusions from the main body, are formed on it. These outgrowths arise at varying intervals and may develop into long, sometimes curved, branches which curl around the inner face of the host-cell wall. After from twenty-four to seventy-six hours of purely vegetative growth this one-celled, usually branched, tube, which ordinarily never penetrates into adjoining host cells, becomes segmented by the formation at irregular intervals of narrow cross walls. In some instances as many as seven segments are produced from a single thallus. These are transformed into reproductive organs.

In *Myzocytium* (Zopf, 1884) the young one-celled thallus early becomes torulose, as if it were being proliferated by a yeastlike budding. Here, however, in contrast to the development in *Lageni-*

dium, no branches are formed. At from twelve to twenty-four hours after infection the vegetative stage is superseded by the reproductive phase. There are now laid down at the constrictions between the successive swellings very thick two-layered refractive cross walls which divide the thallus into a chainlike series of links. All of the segments thus formed become reproductive organs (Fig. 62 A-B, p. 651).

In *Lagenidium*, *Myzocytium*, *Pontisma*, and *Sirolpodium* single-celled thalli which resemble those of *Olpidiopsis* are occasionally observed.

REPRODUCTION

Nonsexual Reproduction

The zoospores of the Olpidiopsidaceae and the Sirolpidiaceae are fully formed in the zoosporangium.

In *Olpidiopsis* (Barrett, 1912b) the maturing sporangium is at first strongly vacuolate. Changes in the contour of the spherical vacuoles occur at the same time that the discharge tube forms. Further stages involve the sudden disappearance of the large vacuoles, with the protoplasm assuming a finely granular, lighter, more homogeneous aspect, and the appearance in some instances of small vacuoles. These vacuoles ultimately vanish, the protoplasm becomes more coarsely granular, and the spore origins appear. The zoospores become more definitely outlined and initiate movement. The discharge tube then opens and the zoospores escape. The exit tube, Barrett believes, secretes an enzyme which aids in penetration, although evidences for mechanical action were also observed. A similar sequence has been described by Butler (1907) in *O. Aphanomyces*, except that in his fungus a heaping of the protoplasm followed the change in contour of the large vacuoles of the resting sporangium. At this stage Butler supposed that the contents became cleaved into relatively large multinucleate masses. Barrett's cytological preparations of sporangia in the resting, vacuolate, condition showed very definitely, however, that in his material the spore centers were already formed and that some fragmentation had been initiated. He considers the heaping described by Butler simply a phenomenon accompanying final stages in the maturation of the spores. According to Barrett, the zoospores are produced simultaneously by division of the protoplasm, and upon the gelatinization and disso-

lution of the tip of the discharge tube the swarmers emerge from the sporangium as vacuolated uninucleate biflagellate structures. Schwartze (1922), on the other hand, from observations only of living material of *O. Saprolegniae*, described the cleavage as progressing rapidly outward from a central vacuole. When the furrows pierced the thin peripheral layer of cytoplasm the vacuole vanished and the outline of the zoospores became distinguishable. Subsequent development involved the appearance of definite polygonal segments followed by contraction of the whole mass. A further contraction resulted in the rounding off and rocking of the individual spores, which escaped after two minutes. This report agrees, in the main, with the classic account of Rothert (1888) of cleavage in *Saprolegnia* and with the recent observations of McLarty (1941a, 1941b) on *Olpidiopsis*.

The zoospores of *Olpidiopsis* are relatively small and numerous. The body, in general, is somewhat ovoid, or reniform with a narrower anterior end. The contents are rather granular. From the forward end two oppositely directed flagella of approximately the same length emerge (Fig. 56 A, p. 593).

In *Pythiella* (Couch, 1935a) the young thallus is invested with a wall and very quickly assumes a rounded or oval shape. Its protoplasm contains large glistening granules, which persist until the thallus reaches almost its mature size. They then vanish, leaving the protoplasm homogeneous save for a few small vacuoles. These soon coalesce to form a large central vacuole, which extends through nearly the whole thallus, including the newly formed discharge tube. At this time, as the furrows of the vacuole stretch toward the periphery, the protoplasm becomes disposed in irregular parietal heaps. The vacuole then suddenly bursts in one or more places, and protoplasm immediately seems to fill the whole sporangium. Shortly afterward the spore initials are visible. This sequence is so similar to that found in the Ectrogellaceae that the fungus might easily be placed in that family, as has been suggested by Couch. The primary spores have no flagella and after discharge from the sporangium encyst at once, forming a group at the tip of the discharge tube (Fig. 58 G, p. 619). From each cyst a biflagellate, "secondary," type of zoospore emerges.

In the primarily marine *Petersenia* the thallus may extend through one or more cells (Fig. 59 D, p. 633). Its contents are refractive and

bear numerous large spherical vacuoles. A homogeneous condition ensues, which is followed by the cleavage of the zoospores. This process has not been observed in its initial phases. The zoospores in their later stages of maturation within the sporangium undergo a rocking and twisting movement very much like that found in *Pythium*. They are minute, grape-seed-like, and laterally biflagellate (Fig. 59 H) (Sparrow, 1934c).

As yet there are not available any precise details concerning the sequence of protoplasmic changes in the developing sporangia of members of the Sirolpidiaceae. Both Petersen (1905) and Sparrow (1934c) state that the zoospores assume motility within the sporangium, emerge by their own efforts, and swim away at once. In *Sirolpidium* (Sparrow, *op. cit.*) the zoospores are minute, narrowly pyriform, somewhat arched or bent, and bear two long oppositely directed anteriorly attached flagella (Fig. 60 I, p. 644). A strongly refractive granule is visible in the front part of the body. In *Pontisma* (Sparrow, *op. cit.*), also, the zoospores are relatively small, narrowly pyriform, and bear a refractive granule at either end. The two oppositely directed flagella arise near the center of the body, or possibly at the fore end.

In the Lagenidiaceae the process of zoospore formation strongly resembles that found in *Pythium*. The relatively large zoospores either are partly formed in the sporangium, as in *Myzocytium* (Zopf, 1884), and complete their maturation in a delicate more or less evanescent vesicle produced at the tip of the discharge tube, or, as in *Lagenidium Rabenhorstii* (Zopf, *op. cit.*), undergo their entire development within the extramatrical vesicle. In the sporangia of *M. proliferum*, a parasite of algae, Zopf noted that, coincidently with the formation of the discharge tube, the protoplasm became separated by small vacuoles into approximately like-sized portions. With the gelatinization of the tip of the tube, these segments of protoplasm emerged to form a globular homogeneous motionless mass at the orifice. No divisions of the protoplasm could be observed at this time. Shortly, however, a slight motion of the whole mass was discernible, accompanied by a contraction away from the wall of the delicate surrounding vesicle. The protoplasm was then cleaved into the same number of parts as was previously observed within the sporangium. As separation continued, the spore origins showed individual motion, and underwent amoeboid changes of shape.

Delicate flagella became visible around the periphery. For a short period after separation the zoospores exhibited a lively swarming within the vesicle, whose delicate membrane eventually deliquesced, releasing the zoospores, which swam away. In *L. Rabenhorstii* (Zopf, *op. cit.*) no separation of the contents of the sporangium could be observed prior to discharge. At maturity the protoplasm flowed out in a continuous stream into a constantly expanding vesicle. There the mass quickly began to rotate and, after a few seconds, was cleaved into parts, each of which in turn assumed individual somewhat amoeboid motion. The zoospores, after forming their flagella and taking on their mature beanlike shape, are liberated upon the disappearance of the vesicle.

Variations from the types of zoospore discharge described by Zopf in *Myzocytium* and *Lagenidium* have been reported by a number of investigators. In *Myzocytium* (Dangeard, 1903b; Thompson, 1934) the zoospores have been observed to form within the sporangium and to initiate motility there. The vesicle was completely absent in the material studied by Thompson, whereas it was quickly evanescent in Dangeard's fungus. In *M. zoophthorum* (Sparrow, 1936a) the zoospores were more or less fully formed in the sporangium and completed their maturation without a surrounding vesicle at the tip of the discharge tube. In *Lagenidium* even more marked departures have been noted. In *L. Cyclotellae*, for example, Scherffel (1925a) has observed the zoospores to be completely formed and moving within the sporangium before discharge. He regards these bodies as primary zoospores. Scherffel (*op. cit.*) also states that in *L. Oedogonii* the zoospores are sometimes formed as in *Pythium*, but that at other times they divide and move within the sporangium, and at discharge form, as in *Achlya*, a clump of cysts at the orifice of the discharge tube. From each of these cysts a secondary zoospore emerges. Couch (1935b) has noted only the *Pythium* type of discharge in *L. Oedogonii*. In *L. Marchalianum* the zoospores may be delimited within the sporangium and complete their maturation in the extra-matrical vesicle, after discharge. A somewhat similar condition has been noted in *L. oophilum* (Sparrow, 1939c). Here, however, the vesicle is apparently completely lacking.

The zoospore in both *Myzocytium* and *Lagenidium* is of the secondary, beanlike, kidney-like, or grape-seed-like, type, with a shallow sinus from which arise two oppositely directed flagella of approxi-

mately equal length. The contents frequently bear numerous refractive granules and a centrally disposed vacuole. The movement is an even gliding, sometimes accompanied by a gentle lateral rocking of the whole body. Couch (1935b) has noted in an unnamed species of *Lagenidium* occurring in *Oedogonium* that the zoospores after coming to rest and encysting may emerge from the cysts again as secondary zoospores and undergo a second swarm period ("repeated emergence"), a further point in which these fungi resemble *Pythium*.

Dangeard (1903b) has given an account of the cytology of *Myzocytium vermicola*, a parasite of nematodes. The young thallus contains numerous nuclei dispersed in a reticulate cytoplasm. After formation of the cross walls the number of nuclei is augmented, but no division figures are found. As the sporangia thus delimited approach maturity, the cytoplasm and nuclei become disposed around a large central vacuole, formed probably by the coalescence of several smaller ones, which were previously visible. Lines of granules then delimit irregular polyhedral areas. The central vacuole disappears and the protoplasm fragments into uninucleate zoospores which are discharged through a tube to the outside.

Sexual Reproduction

Sexual reproduction is known in the Olpidiopsidaceae and the Lagenidiaceae. No well-authenticated occurrence of resting spores of either sexual or asexual origin has been reported in the Sirolpidiaceae. In both the Olpidiopsidaceae and the Lagenidiaceae the resting structure may be asexually developed also (Zopf, 1884; Scherffel, 1925a; McLarty, 1941a).

The process, presumably of a sexual nature, that precedes resting spore formation in *Olpidiopsis* has been studied by numerous observers (Cornu, 1872a; Reinsch, 1878; Fischer, 1880, 1882; Butler, 1907; Barrett, 1912b; Shanor, 1939a, 1939b; McLarty, 1941a, 1941b; etc.). In hypertrophied portions of fungous hyphae in which several parasites are developing, certain thalli of unequal size may become associated, usually in pairs. The larger continues to increase in size and its contents become characterized by the production of numerous fat bodies. The two unequal-sized thalli then secrete cellulose walls and are fused together at one point. A pore develops in the wall of contact, through which the contents of the smaller thallus pass into

the larger, receptive, body. After the contents have fused, an endospore wall of cellulose forms around the larger thallus. At maturity the outer surface of the wall of the receptive thallus bears on it a considerable amount of material, derived, according to McLarty (*opera cit.*), from localized deposits of host protoplasm during maturation. This material is usually laid down unevenly and, as a consequence, produces an exospore layer of spiny, tuberculate, fibrillose, or irregular character. The numerous variations found by McLarty in the character of the exospore occurring in cultures of *O. Achlyae* derived from single zoospores have rightly brought into question the value of the exospore wall as a character in distinguishing species.

The sexual process in *Olpidiopsis* has been examined cytologically by Barrett (1912b) and McLarty (1941b). Both the contributing and the receptive thalli are at first uninucleate, but by repeated simultaneous mitotic divisions they become multinucleate (Fig. 57 H-I, p. 594). The spindles are intranuclear and the number of chromosomes, according to Barrett, is six. Barrett believes that fusion of the nuclei in pairs occurs after the contents of the smaller thallus have passed into the larger one. This is denied by McLarty, who states that, though plasmogamy does unquestionably take place, there are no nuclear fusions. At germination the resting spore becomes converted into a sporangium (Shanor, 1939a; McLarty, 1941b). No evidences of meiosis could be found by McLarty, and this, together with the absence of karyogamy and the frequent maturation of resting spores without previous conjugation, has led him to conclude that sex, at least in *O. Achlyae*, is phenotypically, not genotypically, determined.

Although the sexual reproduction of *Pythiella* bears a superficial resemblance to that of *Olpidiopsis*, it differs in three important particulars. First, the male gametangium forms a definite fertilization tube which pierces the larger, female, gametangium and conveys into it the contents of the male cell. Only a simple pore is formed in *Olpidiopsis*. Secondly, the contents of the female gametangium are clearly differentiated into a central oöplasm and an outer, thinner, layer of periplasm. Lastly, the mature oöspore lies loosely as an independent structure within the female gametangium. It is hoped that further details, especially of the nuclear phenomena, will be forthcoming in regard to this interesting organism.

The sexual reproductive process in the Lagenidiaceae, also, is well known, although cytological details are for the most part lacking. Zopf (1884) showed that adjacent cells of the linklike thallus of *Myzocytium* conjugated. In this process one cell, the antheridium, produced a tube which pierced the walls separating it from the oögonium. The contents of the female structure contracted, moved toward the tip of the tube, and exhibited relatively lively amoeboid motion. With the passage of the protoplasm into the oögonium the female gamete became rounded and nearly quiescent. After fusion the zygote was surrounded by a thick double wall, and a large central globule was formed in the contents. In Zopf's material the oöspore always remained attached to the fertilization tube.

Dangeard (1903b) has studied cytologically the sexual stage of *Myzocytium vermicola*. The gametangia are multinucleate, the somewhat cylindrical male bearing two nuclei, the more rotund female, about eight. The antheridial cell penetrates the female gametangium by means of a tube and discharges its contents. By this time the protoplasm of the female gametangium has contracted and become vacuolate. One male and one female nucleus persist, but the others degenerate. No coenocentrum is visible. After plasmogamy the zygote rounds off in the gametangium, a thin smooth surrounding wall is formed, and the nuclei approach one another. Later, karyogamy occurs and a reticulate exospore is formed. At germination the single large fusion nucleus is replaced by several smaller ones. Meiosis was not observed although, presumably, it took place at this time.

In *Lagenidium Rabenhorstii* (Zopf, 1884), the sex organs, in contrast to those of *Myzocytium*, are ordinarily dioecious, the two plants usually lying parallel in the host. The segment of the thallus which will become the oögonium swells, forming a spherical, ovoid, or fusiform structure. The antheridia are unspecialized segments of the thallus and each forms a tube which makes contact with the oögonium and pierces its wall. The contents of the receptive segment then undergo movement and contract, concentrating at the place of entrance of the fertilization tube. This contraction continues during passage of antheridial material, after which the granular matter in the zygote collects at first into two large refractive masses and then into one. A two-layered smooth colorless wall is now laid down around the zygote. Zopf points out that in *L. Rabenhorstii*, in contrast to higher Phycomycetes, the female gamete is still an am-

phous mass at the time of fertilization and does not round off until later.

The resting spore in both *Myzocytium* and *Lagenidium* lies loosely within the wall of the receptive cell, and closely resembles the oöspore of *Pythium*. The early stages of germination have been observed by Dangeard (1903b) in *M. vermicola*. After resting a few months the oöspore becomes multinucleate and produces a tube through which zoospores may possibly be discharged.

PARASITISM

Specific information on the parasitism of this group is interpolated in the discussions of the various species. A few general remarks, however, are pertinent.

The Lagenidiales are primarily a group of parasitic fungi, although a few, little-known, chiefly marine forms are reported to be capable of living saprophytically in nature. With the exception of *Lagenidium giganteum* (Couch, 1935b), none of the group has been grown extensively on artificial media. Diehl (1935), however, reports the cultivation to maturity of some immature thalli of *Olpidiopsis* which had been removed from their saprolegniaceous host to artificial media. Species of *Olpidiopsis* and *Pythiella* are, with the exception just noted, obligate parasites of aquatic Phycomycetes and of a few fresh-water and marine algae. A recent experimental study of certain species of *Olpidiopsis* (Shanor, 1940) indicates that they are restricted to relatively few host species (see discussion under *Olpidiopsis*, p. 611). *Pseudolpidium* and *Pseudosphaerita*, also, are, so far as is known, obligate parasites of particular hosts. Species of *Petersenia*, a marine genus, may possibly at times be weakly parasitic on certain marine algae (red seaweeds) and initiate the destruction of the alga, but after the death of the host they can unquestionably maintain themselves as saprophytes (Sparrow, 1934c, 1936b). The marine fungus *O. Sphaecellarum*, on the other hand, appears to be a true parasite, invading only the healthy cells of the host, which it stimulates to swell, and accomplishing alone the disintegration of the living contents. When the alga becomes moribund, because of laboratory conditions, the parasite dies (Sparrow, 1936b).

Sirolpodium and *Pontisma*, inhabitants of marine algae, perhaps act as parasites in early stages of infection, but for the major part of their development they live as saprophytes (Sparrow, 1934c, 1936b).

Myzocytium and *Lagenidium* (with the exception of *L. giganteum*)

are at present thought to be obligate parasites of their hosts. They occur primarily as parasites of the Conjugatae, attacking both vegetative and reproductive cells. Other species are found in eelworms, the eggs, embryos, and adults of rotifers, and on pollen grains. As was true of the chytrids, practically no significant experimental work has been attempted to ascertain the range of hosts which a single fungus will attack, and claims of host specificity rest for the most part on observations of findings in nature.

SYSTEMATIC ACCOUNT

LAGENIDIALES

MICROSCOPIC, primarily parasitic aquatic fungi of simple body plan or with a septate mycelial development of slight extent, the thallus endobiotic, holocarpic, forming one or more reproductive organs, without a specialized vegetative system, at first unwalled ("plasmodial") or walled, the walls generally giving a cellulose reaction, infection tube persistent or evanescent, contents in the vegetative stage often having a pale gleaming luster, bearing irregular refractive granules and scattered oil droplets, strongly vacuolate during maturation; zoosporangia forming one or more discharge tubes; the zoospores of the laterally biflagellate type, mono- or diplanetic, produced by successive division within the sporangium or at the orifice of the discharge tube, where they are generally surrounded by a vesicle; resting spore apparently asexually formed, or sexually after conjugation of the receptive thallus with one or more contributing gametangia, fertilization tube and periplasm present or absent, monoecious or dioecious.

Members of the order are most frequently found parasitic in freshwater algae and in other Phycomycetes. A few are parasitic in microscopic aquatic animals and parasitic or saprophytic in seaweeds. One (*Lagenidium giganteum*) has been cultivated on artificial media.

The inclusion of the Olpidiopsidaceae in this order is only tentative, and future work may show it to be untenable. Members of the family certainly appear more closely allied to the Lagenidiaceae than

to the chytrids, where they have been uniformly placed in the past. See the discussion under the Olpidiopsidaceae (below) and the introduction to the Chytridiales (p. 21).

KEY TO THE FAMILIES OF THE LAGENIDIALES

- Thallus always one-celled, infection tube evanescent; zoospores formed within the zoosporangium; resting spore lying free in the host, not formed in a gametangium . . . OLPIIDIOPSIDACEAE, p. 607
- Thallus predominantly multicellular, occasionally one-celled, infection tube frequently persistent; zoospores formed inside the zoosporangium or in a vesicle at the tip of the discharge tube; resting spore formed in a gametangium
- Zoospores formed within the zoosporangium, small, numerous; marine fungi SIROLPIIDIACEAE, p. 642
- Zoospores formed or completing their maturation in a vesicle at the orifice of the discharge tube; fresh-water fungi
LAGENIDIACEAE, p. 647

OLPIIDIOPSIDACEAE

Thallus endobiotic, holocarpic, without a specialized vegetative system, sometimes appearing naked at first ("plasmodial") and somewhat amoeboid, later definitely walled, infection tube not persisting, the walls generally giving a cellulose reaction, forming a single reproductive structure, contents with refractive globules, often strongly vacuolate; sporangium liberating its spores by bursting the wall or forming one or more discharge tubes; zoospores formed in the sporangium, monoplanetic or diplanetic, biflagellate; resting spores endobiotic, thick-walled, apparently asexually formed from the thallus or produced after conjugation of the receptive thallus with one or more small contributing thalli, with or without periplasm and fertilization tubes, upon germination forming zoospores.

Parasites of other water fungi and parasitic or saprophytic in marine algae.

The family includes all endobiotic holocarpic species which form a single sporangium from the thallus and produce, endogenously, biflagellate zoospores. When more is known about the sexual process, if

any, in *Pseudosphaerita* and *Pseudolpidium* it may seem better to place these genera elsewhere.

Scherffel (1925a) has called attention to the resemblance of *Olpidiopsis* to *Lagenidium*, first noted by Zopf (1884). This is found not only in the similarity in flagellation of the spore, the composition of the walls, and the behavior and structure of the contents, but also in the tendency toward diplanetism of the zoospores and the similarity of sexual reproduction.

The thallus in *Olpidiopsis* and *Pythiella* bears at first sight little resemblance to that in *Lagenidium* and *Myzocytium*. In their body form, however, *Lagena* and *Lagenidium oophilum* approximate a species of *Olpidiopsis*, and *Pontisma* and *Sirolpidium* closely approach *Lagenidium*. The essential differences between the two groups appear to rest in the *Pythium* type of diplanetism of a relatively small number of large zoospores in the Lagenidiaceae and the *Saprolegnia* or *Achlya* type of diplanetism of a large number of small zoospores in the Olpidiopsidaceae. These do not seem of sufficient import when compared with the similarities to maintain the groups as distinct orders.

KEY TO THE GENERA OF THE OLPIDIOPSIDACEAE

- Parasitic in aquatic Phycomycetes or in fresh-water or marine filamentous algae
- Resting spore sexually formed after conjugation of thalli; zoospores mono- or diplanetic
 - Zoospores apparently monoplanetic or with poorly defined diplanetism, companion cell not forming a fertilization tube
 - Sporangia predominantly spherical or ellipsoidal, with one, rarely more, discharge tubes OLPIDIOPSIS, p. 609
 - Sporangia predominantly irregularly lobed or tubular, usually with more than one discharge tube
 - PETERSENIA, p. 630
 - Zoospores definitely diplanetic, encysting at the orifice of the discharge tube, companion cell forming a fertilization tube PYTHIELLA, p. 634
- Resting spore apparently asexually formed; zoospores monoplanetic PSEUDOLPIDIUM, p. 636
- Parasitic in Euglenophyceae or Cryptophyceae PSEUDOSPHAERITA, p. 638

OLPIDIOPSIS CORNU

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(Figure 58 A-F, p. 619)

Olpidiopsis (Cornu) Fischer, Jahrb. wiss. Bot., 13:363. 1882; Rabenhorst. Kryptogamen-Fl., 1(4):37. 1892.

Pleocystidium Fisch, Sitzungsber. Phys.-Med. Soc. Erlangen, 16:66. 1884.

Diplophysa Schroeter, in Cohn, Kryptogamenfl. Schlesien, 3 (1):195. 1885.

Pseudolpidium Fischer, pro parte, Rabenhorst. Kryptogamen-Fl., 1 (4): 33. 1892.

Plectrachelus Zopf, sectio *integri* H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):448.

Bicilium H. E. Petersen, Bot. Tidsskrift, 29 (4):357. 1909; Ann. Mycologici, 8:503. 1910.

Pseudolpidiopsis Minden, Kryptogamenfl. Mark Brandenburg, 5:255. 1911 (1915).

Thallus at first naked, later surrounded by a membrane, endobiotic, holocarpic, forming the rudiment of the sporangium, the receptive thallus, or the contributing thallus (companion cell); sporangium spherical or ellipsoidal, smooth-walled or spiny, nontubular and unlobed, with from one to several discharge tubes; zoospores formed within the sporangium, biflagellate, without well-defined diplanetism; resting spore thick-walled, smooth or spiny, formed asexually or after conjugation of the receptive thallus with from one to several smaller contributing thalli, upon germination functioning as a sporangium.

Primarily parasites of fresh-water fungi, but also occurring in fresh-water and marine algae.

The zoospore was said by Cornu to be posteriorly uniflagellate. Fischer (1882) described it as biflagellate in the species studied by him. His generic description (1892) allows for both types. Schroeter's generic description (1893) mentions only the biflagellate type, as does that of Minden (1915).

Very recent work by Shanor (1939a, 1939b) and McLarty (1939, 1941a) with single-spore cultures of various species of *Olpidiopsis* and of forms which would ordinarily be placed in Fischer's genus *Pseudolpidium* has shown all these fungi to be species of *Olpidiopsis*.

Fischer's genus is, therefore, reduced to synonymy, in part. *Ps. Pythii* and *Ps. gracile* await further study to determine their affinities.

As here understood, the genus includes all forms with unlobed or nontubular endobiotic holocarpic thalli, with biflagellate zoospores, with sporangia bearing one to several discharge tubes, and with resting spores produced either asexually or after conjugation of thalli. In the past the marine forms have been referred both to *Pleotrichelus* (Petersen, *loc. cit.*) and to *Petersenia* (Sparrow, 1936b), but they differ from the first in having biflagellate zoospores and from the second in having unlobed nontubular sporangia. *Peronium aciculare* Cohn (1853) may possibly have been a species of this genus, but it is too imperfectly known to be considered here.

Butler (1907), Barrett (1912b), Scherffel (1925a), and Diehl (1935) all describe what might be considered a poorly defined type of diplanetism of the zoospores. After the zoospores escape from the sporangium there is a short period of motility, which, in *Olpidiopsis Saprolegniae* and *O. Schenkiana*, may include slight amoeboid motion; this is followed by a period of quiescence accompanied by retraction of the flagella. During the rest period contractile vacuoles may appear in the plasma. At its conclusion the flagella initiate movement and elongate, and the spore, after rocking for a while, once more assumes motility. No encystment occurs, and the primary zoospore is interpreted as having been directly transformed into the secondary swarmer. Whether such significance should be accorded what is after all only an interval of rest unaccompanied by encystment or change of shape of the zoospore is problematic. Scherffel considers *Olpidiopsis* to exhibit a partial suppression of the primary swarm stage, which reaches its end point in the *Pythium*-type, where only secondary zoospores appear. As supporting evidence he cites the behavior of the zoospores of *O. Oedogoniarum*, which emerge sometimes as in *Achlya*, sometimes as in *Pythium*. It is important, however, that unquestionable proof be presented that only one species of fungus is involved in such occurrences.

Scherffel has also called attention to the close resemblance of *Olpidiopsis* to *Myzocytium*; he regards *Olpidiopsis* as providing a connecting link between the Ectrogellaceae and the Lagenidiales. Indeed, in *O. Oedogoniarum*, where, in contrast to other species, the resting spore lies loosely in the receptive thallus, this resemblance is extremely close. A constant difference between the two groups is to

be found, according to Scherffel, in the persistence of the infection tube on the thallus of the lagenidiaceous fungus, whereas in *Olpidiopsis* the thallus is established in monad-like fashion and lies wholly free in the host cell.

Whether or not host specialization actually exists in all species of *Olpidiopsis* is not known with certainty. Experimental work here, as in other fungi, is hampered by imperfect knowledge of optimum conditions for resistance of the host plants. Shanor (1940) summarizes an extensive study of the host range of certain species thus:

A study of the host range of certain species of *Olpidiopsis* which occur as parasites of the water molds has been made in which twenty-five species representing eight genera of the Saprolegniaceae were used as possible hosts. In all, two hundred and sixty-four single host exposures have been made. Two species, *Olpidiopsis varians* and *O. fusiformis*, confine their parasitism to species of *Achlya*. *Olpidiopsis varians* parasitizes *Achlya flagellata* and *A. proliferoides* very vigorously and *A. racemosa* and *A. colorata* only to a very slight degree. *Olpidiopsis fusiformis* parasitizes *A. imperfecta* and *A. Klebsiana* vigorously and *A. racemosa* only slightly. Two other species, *Olpidiopsis Saprolegniae* and *O. incrassata* were found to parasitize all species of *Saprolegnia* exposed to them. *Olpidiopsis Saprolegniae* is also capable of parasitizing *Isoachlya anisospora*, *I. unispora* and *I. eccentrica* while *O. incrassata* has parasitized only *I. anisospora* and *I. unispora*. *Olpidiopsis incrassata* is considered a natural parasite of *Saprolegnia* The host range of *Olpidiopsis luxurians* appears to be confined to a single species, *Aphanomyces laevis*.

KEY TO THE SPECIES OF OLPIDIOPSIS

In the hyphae of fresh-water Phycomycetes

Parasitic in *Saprolegnia*; resting spore predominantly spherical
O. Saprolegniae, p. 612

Parasitic in other Phycomycetes; resting spore spherical or ellipsoidal

Parasitic in *Achlya* and *Isoachlya*; resting spore predominantly spherical, wall either spiny, tuberculate, fibrillar, or undulate

Companion cell smooth-walled

Resting-spore wall spiny; companion cell always present
O. fusiformis, p. 615

Resting-spore wall spiny, tuberculate, fibrillar, or undulate; companion cell present or absent *O. Achlyae*, p. 616

- Companion cell spiny
- Spines short
 - Spines short, tenuous, the outer wall not continuous with that of the resting spore *O. index*, p. 617
 - Spines coarse, the outer wall continuous in most cases with that of the resting spore *O. varians*, p. 618
 - Spines very long and rodlike *O. spinosa*, p. 618
- Parasitic in *Achlya* (and *Saprolegnia*?); resting spores predominantly ellipsoidal, the walls tuberculate or undulate, never spiny *O. incrassata*, p. 620
 - O. major*, p. 621
 - O. vexans*, p. 621
- Parasitic in *Aphanomyces laevis* *O. luxurians*, p. 622
- In fresh-water or marine algae
 - In fresh-water algae (Chlorophyceae); discharge tubes generally occurring singly
 - Resting spore and companion cell smooth-walled
 - Resting spore filling the receptive cell; sporangia broadly or narrowly ellipsoidal; in Conjugatae. *O. Schenkiana*, p. 622
 - Resting spore lying loosely in the receptive thallus; sporangia elongate, ovoid, saclike; in *Oedogonium*
 - O. Oedogoniarum*, p. 624
 - Resting spore covered with long fibrils or spines, companion cell smooth-walled
 - Resting spore covered with long delicate radiating fibrils
 - O. fibrillosa*, p. 625
 - Resting spore covered with spines
 - Spines slender, companion cell long, vermiform
 - O. appendiculata*, p. 625
 - Spines coarse, companion cell spherical *O. Zoppii*, p. 626
 - In marine algae, sporangia spherical or ellipsoidal, with from one to seven radiating discharge tubes; resting spore spherical or ellipsoidal, smooth-walled *O. Andreei*, p. 626

OLPIDIOPSIS SAPROLEGNIAE (Braun) Cornu

Ann. Sci. Nat. Bot., V, 15:145, pl. 3, fig. 10. 1872

(Figure 58 A-B, p. 619)

Chytridium Saprolegniae Braun, Monatsber. Berlin Akad., 1855:384;
Abhandl. Berlin Akad., 1855:61, pl. 5, fig. 23. 1856.

Diplophysa Saprolegniae (Cornu) Schroeter, in Cohn, Kryptogamenfl.
Schlesien, 3 (1):195. 1885.

Pseudolpidium Saprolegniae Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):35, fig. 3 a-b. 1892.

Olpidiopsis echinata H. E. Petersen, Bot. Tidsskrift, 29(4):405, fig. 28a. 1909; Ann. Mycologici, 8:540, fig. 28a. 1910.

Sporangium predominantly spherical, subspherical, ovoid, or ellipsoidal, up to 150 μ in diameter (45–50 \times 3–36 μ when ellipsoidal), generally terminal, occasionally intercalary in the hypertrophied host filaments, wall thin, smooth or spiny, colorless, discharge tubes from one to three, narrowly cylindrical, of variable length; zoospores ovoid or ellipsoidal, 2–4 μ in length, with two apical or subapical oppositely directed flagella; resting spore spherical, 47–107 μ in diameter, colorless or somewhat brownish, with a fairly thick wall, the outer surface densely covered with slender sharp spines about 5–10 μ in length, contents with globules, germination not observed; companion cells from one to two, ovoid or nearly spherical, 18–28 μ in diameter, wall thin, smooth, colorless.

Parasitic in filaments of *Saprolegnia ferax*, Nägeli (1846), Braun (*loc. cit.*), Pringsheim (1860:205, pl. 24, fig. 15), GERMANY; *Saprolegnia* sp., Cornu (*loc. cit.*), Dangeard (1890–91b:88, pl. 4, figs. 5–8), FRANCE; *Saprolegnia* sp., Sorokin (1883:27, fig. 27), EUROPEAN RUSSIA, ASIATIC RUSSIA; *S. dioica*, *S. monoica*, Petersen (*loc. cit.*), DENMARK; *Saprolegnia* sp., Barrett (1912b:232, pl. 23, figs. 2, 8–9, 21 A, pl. 24), *Achlya imperfecta*, *A. flagellata*, Coker (1923:184, pl. 62, figs. 7–10), *Achlya* sp., Sparrow (1932b:270, text fig. 1c; 1933c:515), Shanor (1940), UNITED STATES; *Saprolegnia monilifera*, Tokunaga (1933a:24, pl. 2, fig. 9), JAPAN; host (?), Forbes (1935b:3), ENGLAND.

For convenience the records of *Pseudolpidium Saprolegniae* are listed separately:

Parasitic in hyphae of *Saprolegnia monoica*, *S. Thureti*, *S. astero-phora*, Fischer (*loc. cit.*), *Saprolegnia* sp., Pringsheim (1860:205, pl. 24, fig. 14), *Saprolegnia* sp., Schroeter (1885:195), Minden (1915:267), GERMANY; *Achlya* (*Saprolegnia* ?) *prolifera*, Cienkowski (1855:801, pl. 12, fig. 8 and others?), RUSSIA; *Saprolegnia* sp., Sorokin (1883:27, fig. 28), ASIATIC RUSSIA; *Saprolegnia* sp., Constantineanu (1901:372), RUMANIA; *Achlya racemosa*, H. E. Petersen (1909:406; 1910:541, fig. 18d), DENMARK; *Saprolegnia* sp., Valkanov (1931a:361), BULGARIA; (?) *Saprolegnia Thureti*, Tokunaga (1933a:22, pl. 2, fig. 5), JAPAN.

Butler (1907:131), Sawada (1912), and Domján (1936:52) record the fungus from the sporangial stage alone.

Constantineanu's record can be accepted only with reservation, since the ornamentation of the resting spore is not described.

Marked hypertrophy of the host filament has been noted by all observers of the species. Diehl (1935) observed that the form assumed by the infected hyphae depended upon the size and abundance of protoplasm in the host hypha and the number of parasites infecting it. Considerable increase in diameter and cessation of apical growth occurred in regions harboring the parasite. These "galls" assumed various configurations in agar cultures. Under conditions of culture the discharge tubes of the sporangia reached great lengths. Diehl also found that in the later stages of development isolated parasites on agar reached maturity and discharged their zoospores.

Coker (*loc. cit.*) has noted in a single sporangium that the contents were discharged before cleavage of the spores had been completed. The protoplasm remained at the orifice, and after fifteen minutes the spore initials assumed a rocking movement. Eventually, they became separate entities and swam away. This may not be typical of zoospore discharge, but if it is it affords additional evidence of the diplanetic nature of the zoospores in the genus. Coker's material also possessed resting spores in which the wall sculpturing varied from low warts to definite spines.

Cornu has retained Braun's specific name even though it is now impossible to tell to what species the German fungus belonged.

Tokunaga's collection is queried above because of the unusually coarse spines on the "resting spore" (sporangium). The sporangia are ellipsoidal, 34-120 μ in longer diameter, the zoospores ovoid, $4 \times 2 \mu$, apically and laterally flagellate, and the resting spores spherical or ellipsoidal, 64-87 μ in diameter, with the wall covered by scattered spines. These spines are described as "fine" in the text, but are far coarser and longer than those figured by Fischer for his fungus.

In view of the extensive cross-inoculation studies by Shanor (1940) which indicate that this species is confined to *Saprolegnia* and *Isoachlya*, the records of *Olpidiopsis Saprolegniae* on *Achlya* are open to question.

OLPIDIOPSIS SAPROLEGNIAE var. *LEVIS* Coker, The Saprolegniaceae,
p. 185, pl. 62, figs. 1-6. Chapel Hill, N. C., 1923.

"Sporangia spherical to elliptic, smooth, very variable in size and number, usually occupying the swollen ends of hyphae but not rarely also in intercalary swellings; emptying by one or two tubes which penetrate the host's wall but go little beyond and are usually short, at times however as long or longer than the diameter of the sporangium; spores very minute and numerous, probably with two cilia, swimming rapidly, emerging at first through internal pressure and probably showing the same sequence as described in preceding species but not all stages observed. Oogonia elliptic to nearly spherical, with the wall rather thick and quite smooth and even; antheridial cells smaller than the oogonia, smooth, thin-walled, one or two attached to each oogonium, their contents usually disappearing entirely by the time the oogonia are mature" (Coker, *loc. cit.*).

Parasitic in *Saprolegnia ferax*, *S. monoica*, UNITED STATES.

OLPIDIOPSIS FUSIFORMIS Cornu

Ann. Sci. Nat. Bot., V, 15:147, pl. 4, figs. 1-4. 1872

Pseudolpidium fusiforme Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):
35. 1892.

Olpidiopsis minor Fischer, *ibid.*, p. 39. 1892.

Pseudolpidium stellatum Sawada, Special Bull. Agr. Exp. Sta. Formosa,
3:70, pl. 8, figs. 11-16. 1912.

Sporangium causing swelling of the host hypha, usually fusiform, also ellipsoidal or cylindrical, 45-350 μ long by 18-78 μ in diameter, with a thin, smooth or spiny, colorless wall, variable in size; zoospores ovoid, 4 μ long by 2 μ wide, biflagellate; resting spore frequently ellipsoidal, or spherical, colorless, thick-walled, the outer surface sparingly covered with broad subulate spines which are joined at their bases to form a reticulum, contents with globules, germination not observed; companion cell spherical, smooth-walled, smaller than the resting spore.

Parasitic in hyphae of *Achlya leucosperma*, *A. racemosa*, *Achlya* sp., CORNU (*loc. cit.*), FRANCE; *Achlya racemosa*, Reinsch (1878:304, pl. 17, figs. 1-4), *Achlya* sp., Fischer (*loc. cit.*), MINDEN (1915:265), GERMANY; *Achlya polyandra*, E. J. Butler (1907:134, pl. 9, figs. 8-11),

INDIA; *Achlya* sp., H. E. Petersen (1909:406; 1910:541, fig. 18g), DENMARK; *Achlya* sp., Sparrow (1932b:270, fig. 1 f-g), *A. imperfecta*, *Achlya* spp., Shanor (1939b:text fig. 2, pl. 25, fig. 2; 1940), UNITED STATES; *Achlya flagellata*, *A. flagellata* var. *yekoensis*, *A. racemosa*, Tokunaga (1933a:23, pl. 2, figs. 6-8), JAPAN.

For convenience the records of *Pseudolpidium fusiforme* are listed separately:

Parasitic in hyphae (not confined to the apex) of *Achlya polyandra*, *A. prolifera*, Fischer (*loc. cit.*), host (?), Minden (1915:267), GERMANY; *Achlya flagellata*, *A. flagellata* var. *yekoensis*, *A. racemosa*, Tokunaga (1933a:21, pl. 2, figs. 1-2), JAPAN; *Achlya prolifera*, *Achlya* sp., Sawada (see Tokunaga, *op. cit.*, p. 22), FORMOSA; *Achlya* sp., Sparrow (1936a:425), ENGLAND.

Sorokin (1883:27, fig. 27) assigns oblong sporangia found in *Achlya* and *Saprolegnia* in European and Asiatic Russia to this species.

Because of the great differences in the shape and the size of the sporangia and in the size of the resting spore as described by various investigators the data were not all included in the diagnosis. Briefly, according to these observers, they are as follows:

Reinsch (*loc. cit.*): Sporangia oblong, irregularly cylindrical or ellipsoidal, 22.4-39.3 μ (in diameter?); resting spore colorless, 22.4-39.3 μ ; companion cells from one to three, ellipsoidal, 16.8-22.4 μ in diameter.

Butler (*loc. cit.*): Sporangia spherical, up to 80-120 μ in diameter; resting spore yellowish brown, 40-60 μ in diameter, with a single globule; companion cell smaller.

Sparrow (*loc. cit.*): Sporangia ovoid or ellipsoidal, occasionally with small spines, 21.7 μ long by 10.4 μ wide; resting spore colorless, 34.5-52.6 μ in diameter, spines 10.5 μ long; companion cell 18.5 μ in diameter.

Tokunaga (*loc. cit.*): Sporangia spherical or ellipsoidal, sometimes elongate, 45-97 μ long, 25-50 μ wide, with from one to two discharge tubes; resting spore spherical, 32-52 μ in diameter, yellowish brown; companion cells from one to two, 16-24 μ in diameter.

Sawada (see Tokunaga, 1933a:22): Sporangia not observed; resting spore ovoid to globose, hyaline or yellowish, 24-100 μ in diameter, the wall covered with conical sharp-pointed spines 9-24 μ long.

OLPIDIOPSIS ACHLYAE McLarty

Bull. Torrey Bot. Club, 68:62, figs. 1-26. 1941

"Zoosporangia solitary or numerous, usually localized in a terminal or intercalary swelling of the host filament, slightly brown and granu-

lar, enclosed at maturity by a cellulose wall, smooth or covered with fine or coarse non-cellulose bristles; spherical, oval, ellipsoidal or elongate, variable in size, $13.2\text{--}112.4 \mu$ diam. $\times 115.0\text{--}666.4 \mu$; one to three exit tubes which may extend considerably beyond the surface of the host filament. Zoospores hyaline with numerous small granules, oval, spherical, or somewhat reniform, $2.3\text{--}5.7 \mu$ \times $2.9\text{--}4.3 \mu$, usually about $4.2 \times 3.1 \mu$, with two approximately equal flagella attached laterally near the anterior end. Resting spores sexual and asexual or parthenogenetic, spherical or oval, $22.8\text{--}122.4 \mu$ (usually about $50.0 \times 41.0 \mu$), brown, with several or commonly one, large refringent globule. Endospore composed of cellulose, smooth, $1.0\text{--}1.5 \mu$ in thickness. Exospore not composed of cellulose, varying from $1.0\text{--}11.4 \mu$ in thickness, with warty protuberances, small or large, narrow or broad-based spines, hair-like fibrillae or with an entire, undulant or slightly serrate margin. Male cells, when present, may or may not discharge contents into female thallus, similar in appearance to zoosporangia, one to three attached to one female thallus, spherical or oval, thin-walled, smooth, sometimes embedded in the exospore. Resting spore in germination transformed into a sporangium liberating zoospores by means of an exit tube" (McLarty, *loc. cit.*).

Parasitic in *Achlya flagellata*, CANADA (ONTARIO).

Possibly, as McLarty suggests, this fungus is referable to *Olpidiopsis fusiformis*.

OLPIDIOPSIS INDEX Cornu

Ann. Sci. Nat. Bot., V, 15:145, pl. 3, fig. 11. 1872

Sporangium narrowly ellipsoidal, with a thin smooth colorless wall and a single discharge tube; zoospores not observed; resting spore spherical, with a somewhat thickened wall densely covered with short slender spines; companion cell spherical, sparingly covered with short slender spines.

Parasitic in *Achlya* sp. (preparations), FRANCE; *Saprolegnia*, Sorokin (1883:29, fig. 30), ASIATIC RUSSIA.

Differing from *Olpidiopsis Saprolegniae* in the spiny wall of the companion cell and, to a lesser degree, in the more narrowly ellipsoidal sporangium.

OLPIDIOPSIS VARIANS Shanor

J. Elisha Mitchell Sci. Soc., 55:171, text figs. A-E, pl. 24, figs. 1-13.

1939

(Figure 58 D-F)

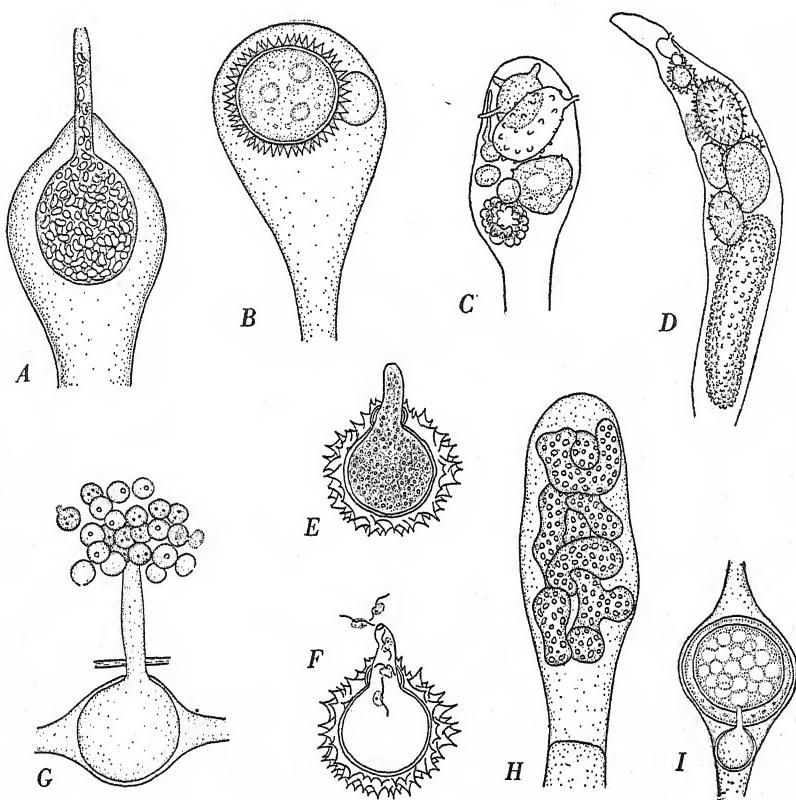
"Zoosporangia single to many, formed either in terminal or intercalary swellings of the host hypha, elliptical, oval, or spherical, extremely variable in size from 60 by 40 μ up to 350 by 140 μ , frequently about 200 by 80 μ , walls giving cellulose reaction with chloro-iodide of zinc, smooth to very spiny, spines slender and somewhat conical, up to 7 μ long, not giving the cellulose reaction; exit tubes commonly one to three (as many as five have been observed). Zoospores oval to elongated, 3.8-4.6 μ long by 2.3-3.0 μ in diameter, usually about 4.2 by 2.8 μ , biciliate, cilia of about equal length, measuring from about 4.2 to 4.6 μ . Oogonia yellowish-brown and very variable in size, spherical, with usually one but sometimes two antheridia attached, 26 to 83 μ in diameter (not including spines), averaging between 52 and 61 μ ; exospore wall colorless to yellowish, about 1.2 μ thick, bearing usually coarse abruptly tapering spines which measure up to 8.6 μ long and have a reticulum connecting them, not giving the cellulose reaction; endospore wall yellowish-brown, about 1.7 μ thick, smooth, and giving the cellulose reaction. Antheridia (companion cells) usually spherical, 17 to 30 μ in diameter, commonly about 26 μ , wall occasionally smooth but typically covered by scattered spines similar to those on the oogonia but much shorter, 1.7 μ at the longest, outer part of wall bearing spines usually colorless, inner wall having a slightly yellowish cast. Contents of antheridia pass into oogonia and antheridia on mature oogonia are empty. Germination takes place in this species by means of a germination tube which usually penetrates the companion cell. Biciliate zoospores are produced when the resting spore germinates" (Shanor, loc. cit.).

On *Achlya flagellata* Coker, UNITED STATES (NORTH CAROLINA).

OLPIDIOPSIS SPINOSA Tokunaga

Trans. Sapporo Nat. Hist. Soc., 13(1):25, pl. 2, figs. 10-11. 1938

Sporangium ellipsoidal or cylindrical, mostly 92-198 μ long by 34-61 μ broad, with from one to two discharge tubes; host hypha distended; zoospores ellipsoidal or somewhat elongate, provided with

FIG. 58. *Olpidiopsis*

A-B. Olpidiopsis Saprolegniae (Braun) Cornu ($\times 367$) in *Saprolegnia* sp.: A, sporangium in swollen tip of hypha; B, spiny resting spore with companion cell. C. *Olpidiopsis vexans* Barrett ($\times 60$), tip of hypha of *Saprolegnia litoralis* containing smooth- and rough-walled sporangia and a rough-walled resting spore with its companion cell. D. *Olpidiopsis varians* Shanor ($\times 60$), tip of hypha of *Achlya flagellata* bearing smooth-, spiny-, and rough-walled zoosporangia and a resting spore with its companion cell. E-F. Germination of resting spore of *Olpidiopsis varians* Shanor ($\times 184$). G. *Pythiella vernalis* Couch ($\times 1000$), discharged sporangium in hypha of *Pythium*; secondary zoospores are beginning to emerge from cysts. H. *Petersenia irregularare* (Constantineanu) Sparrow ($\times 280$), thallus in tip of *Achlya* hypha. I. *Pythiella vernalis* Couch ($\times 1000$) in hypha of *Pythium*, resting spore with small antheridial cell.

(B, Sparrow, 1932b; C-D, Shanor, 1939b; E-F, Shanor, 1939a; G, I, Couch, 1935a)

an anterior and a lateral flagellum; resting spore spherical, 51–73 μ in diameter (without the spines), with a thickened dark or silvery wall, the outer surface covered with numerous hyaline rodlike sharp-pointed spines 9.6 μ long, germination not observed; companion cell spherical, 25.2–32.4 μ in diameter, with a thin wall, the outer surface densely covered with long rodlike sharp spines.

Parasitic in hyphae of *Achlya flagellata*, sometimes occurring with "*Pseudolpidium fusiforme*" and "*Olpidiopsis minor*," JAPAN.

OLPIDIOPSIS INCRASSATA Cornu

Ann. Sci. Nat. Bot., V, 15:146, pl. 4, fig. 12. 1872

Pseudolpidium incrassata (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):37. 1892.

(?) *Olpidiopsis major* Maurizio, Jahresbericht Naturforsch. Gesell. Graubündens, Chur, 38:15, pl. 1, figs. 4–9. 1895.

(?) *Olpidiopsis vexans* Barrett, Ann. Bot. London, 26:231, pl. 23, figs. 15, 19–21, pl. 24, figs. 26–27, 32–39, pl. 25, figs. 40–42, 44, 47–71, pl. 26, fig. 75. 1912.

Sporangium ellipsoidal or subspherical, wall thin, smooth, colorless, discharge tube single, stout or narrowly cylindrical; zoospores not observed; resting spore ellipsoidal, yellowish brown, with a thick strongly undulating wall, germination not observed.

Parasitic in *Achlya racemosa*, Cornu (*loc. cit.*), FRANCE; *Achlya* sp., Sparrow (1933c:515), UNITED STATES.

Sorokin's fungus (1883:29, fig. 29) referred to this species is not identifiable.

Only one doubtful instance of the presence of a companion cell on a resting spore was noted by Cornu, and the fungus has, consequently, been referred to *Pseudolpidium* by Fischer. The resting spores observed by Sparrow were nearly colorless.

Shanor (1940) has indicated that he will bring forth evidence to prove that *Olpidiopsis major* and *O. vexans* are synonymous with Cornu's species. His experimental work has shown, however, that the material on which he bases his study is confined to *Saprolegnia*. This agrees with the findings of Maurizio and Barrett, but is contrary to the observations of Cornu and Sparrow, who have found the fungus on *Achlya*. There can be little doubt that Shanor has studied his material far more extensively. In view, however, of the host specific-

ity clearly demonstrated by Shanor in his own material and in other species of the genus, it is possible that different physiological strains or even different species are involved. Because of the lack of a specific description by Shanor of his fungus the descriptions of *O. major* and *O. vexans* are appended and the names included in the key to the species.

OLPIDIOPSIS MAJOR Maurizio

Jahresbericht Naturforsch. Gesell. Graubündens, Chur, 38:15, pl. 1, figs. 4-9.
1895

Sporangium spherical and 23.5-80 μ in diameter or ovoid and 22-62 μ wide by 70-124 μ long, wall smooth, thin, colorless, generally in the swollen apical part of the host hypha, with from one to four (mostly two) narrowly cylindrical discharge tubes of variable length; zoospores ovoid, biflagellate, emerging simultaneously through the discharge tubes; resting spore ellipsoidal, 74.5-105 μ long by 30-50 μ broad, thick-walled, the outer wall light yellow and strongly undulate, germination not observed; companion cells from one to four (mostly two), spherical and 18.5 μ in diameter or somewhat ellipsoidal and 15.5-21.5 μ wide by 28-31 μ long, wall smooth, thin, colorless.

Parasitic in *Saprolegnia Thureti*, *S. hypogena* var. V, SWITZERLAND.

See remarks under *Olpidiopsis incrassata*, page 620.

OLPIDIOPSIS VEXANS Barrett

Ann. Bot. London, 26:231, pl. 23, figs. 15, 19-21, pl. 24, figs. 26-27, 32-39,
pl. 25, figs. 40-42, 44, 47-71, pl. 26, fig. 75. 1912
(Figure 58 C, p. 619)

"Sporangia single or multiple, formed in terminal or intercalary swellings of the host hyphae, elliptical, oval, or spherical, very variable in size, up to 176 μ in diameter, with smooth, colorless membrane, colorless contents, and one to several unbranched exit tubes; zoospores elongated, slightly inequilateral, with two cilia attached at or near the anterior end. Oospores dark grey, with one, sometimes two, antheridial cells; oospores surrounded by a thick endospore and a thin warty exospore, spherical to oval, sometimes elliptical, up to 116 \times 84 μ , average 50 μ in diameter; antheridia spherical, less

commonly oval, average diameter 20 μ , with a smooth, colorless wall. Germination of oospores not observed" (Barrett, *loc. cit.*).

In hyphae of *Saprolegnia ferax*, Barrett (*loc. cit.*), *S. monoica*, Graff (1928:159), UNITED STATES; *Saprolegnia* sp., Fischer (as *Olpidiopsis Saprolegniae*; 1892:38), Minden (1915:263), GERMANY; *Saprolegnia* sp., *Achlya* sp., Petersen (as *Olpidiopsis Saprolegniae*; 1909:404; 1910:539, fig. 28b), DENMARK.

See remarks under *Olpidiopsis incrassata*, page 620.

OLPIDIOPSIS LUXURIANS Barrett

Ann. Bot. London, 26:231, pl. 23, figs. 1, 5-7, 10-14, 17, 21b, 22, pl. 24, figs. 24-25, 28-30, pl. 25, figs. 43, 45, pl. 26, figs. 74, 76-90. 1912

"Sporangia single or multiple, formed in terminal or intercalary swellings of the host hyphae, oval to spherical, very variable in size, with one to three exit tubes extending considerably beyond the wall of the host; zoospores rather small, elongated, with two cilia attached at or near the anterior end. Oospores spherical, with one or two, rarely three, antheridia, with a thick endospore and a thin exospore provided with numerous conical spines up to 2.5 μ in length; oospores 25-50 μ in diameter, contain one or more large oil globules; antheridia spherical, frequently oval to elliptical, 10-25 μ in diameter, with a smooth colorless wall. Germination of oospores not observed" (Barrett, *loc. cit.*).

Parasitic in *Aphanomyces laevis*, UNITED STATES.

From the coarseness of the spines on the resting spore, the species appears to be intermediate between *Olpidiopsis fusiformis* (*minor*) and *O. Saprolegniae*. Barrett states it could not be transferred to hosts on which *O. minor* (*fusiformis*) had been reported. This has been verified by Shanor (1940).

OLPIDIOPSIS SCHENKIANA Zopf

Nova Acta Acad. Leop.-Carol., 47:168, pl. 15, figs. 1-32. 1884

Pleocystidium parasiticum Fisch, *Sitzungsber. Phys.-Med. Soc. Erlangen*, 16:67, pl. 1, figs. 24-39. 1884.

Pseudolpidiopsis Schenkiana (Zopf) Minden, *Kryptogamenfl. Mark Brandenburg*, 5:257. 1911 (1915).

Sporangium broadly or narrowly ellipsoidal, rarely spherical, often somewhat curved, wall thin, smooth, colorless, discharge tube usually single, fairly broad, variable in length, often long and tortuous, arising laterally on ellipsoidal sporangia, occasionally causing swelling of the infected cell; zoospores from eight to fifty, grape-seed-like, biflagellate, with refractive colorless globules in the plasma, formed in the sporangium and either emerging through the tube and swimming directly away or first undergoing amoeboid motion at the orifice and without encystment being directly transformed into the secondary zoospore, which swims away; resting spore spherical or ellipsoidal, with a smooth thickened brownish or colorless wall and a large globule in the contents, upon germination producing a discharge tube and functioning as a sporangium; companion cells from one to four, sessile or attached by a short beak, spherical, smaller than the resting spore, thin-walled, colorless.

Often in company with other parasites in vegetative cells, gametangia, and, rarely, zygosores of *Mesocarpus* sp., *Mougeotia* sp., *Spirogyra* sp., Zopf (*loc. cit.*), Fisch (*loc. cit.*), Minden (*loc. cit.*), GERMANY; *Spirogyra* sp., de Wildeman (1890:24; 1896b:31, pl. 2, figs. 1-12, 15-17), (coll. Marchal) de Wildeman (1890, 1896b [LUXEMBOURG]), BELGIUM; *Spirogyra* sp., Constantineanu (1901:375), RUMANIA; *Spirogyra* sp., E. J. Butler (1907:135, pl. 10, figs. 11-13), INDIA; *Spirogyra* sp., *Mougeotia* sp., Scherffel (1925a:104, pl. 4, figs. 191-198), Krenner (1935), Domján (1936:52, pl. 1, figs. 172-173, 182-184), HUNGARY.

From Fisch's, de Wildeman's, and Scherffel's reports, the fungus is strongly nucleophagous.

In spite of the numerous observations there seem to be no records of sizes of the parts except in Domján. Here the sporangium is interpreted from the Hungarian text to be 40-60 μ long by 15-32 μ wide. Apparently, zoospore discharge is of the "Achlya type." Scherffel and presumably Domján, also, have noted the formation of a "secondary" sporangium within the primary structure.

Zopf's seemingly incorrect observations on the flagellation of the zoospore led Minden to erect *Pseudolpidiopsis* for the disposition of this species.

OLPIDIOPSIS OEDOGONIARUM (de Wild.) Scherffel

Arch. Protistenk., 52:103, pl. 4, figs. 199-207c, pl. 5, figs. 207d-208. 1925

Olpidiopsis fusiformis var. *Oedogoniarum* Sorokin, Arch. Bot. Nord France, 2:30, fig. 31. 1883 (separate).¹

Olpidium Oedogoniarum (Sorokin) de Wildeman, Ann. Soc. Belge Micro. (Mém.), 18:154, pl. 6, figs. 9-10. 1894.

Sporangium lying free in the host cell, elongate, ovoid, saclike, broadly fusiform or reniform, with broad rounded ends, 15-50 μ long by 5-8 μ in diameter, the long axis parallel with that of the algal cell, with a single lateral median (rarely otherwise placed) tapering discharge tube 4-6 μ long by 3-4 μ wide which, funnel-like, projects slightly extramatrically, wall thin, colorless, smooth; zoospores oval in outline, dorsally arched, with hyaline plasma containing refractive granules and a bright spot, 5 μ long, with two equal, opposed flagella arising from the flattened ventral surface, generally emerging from the sporangium as partly formed bodies which undergo their final maturation at the tip of the discharge tube, escaping rarely as distinct attenuated biflagellate motile spores which encyst at the mouth of the discharge tube and after a period of rest emerge from the cysts (3 μ in diameter) as biflagellate zoospores with a single globule, (shape?), 5 μ long, movement "dancing" or an even swimming; resting spore spherical or subspherical, 13 μ by 10 μ , lying loosely within a saclike smooth oögonium, with a thick smooth colorless wall, the contents with numerous small refractive globules and a single large eccentric lustrous fat body, without periplasm, germination not observed; companion cell elongate, saclike, or subspherical, 10 μ in diameter, smooth-walled, attached to the wall of the oögonium by a beaklike projection or sessile on it.

In *Oedogonium* sp., Sorokin (*loc. cit.*), ASIATIC RUSSIA; *Oedogonium* sp., de Wildeman (*loc. cit.*), FRANCE; *Oedogonium* sp., Scherffel (*loc. cit.*), HUNGARY; *Oedogonium* sp., Sparrow (1933c:516, text fig. I, 9-10), UNITED STATES.

According to Scherffel, the infecting zoospore after coming to rest on the host wall forms a hemispherical appressorium, from the base of which a delicate penetration tube is produced. After discharge of the contents into the host the external parts of the infecting zoospore

¹ See also Sorokin, *Revue Mycologique*, 11:84, pl. 80, fig. 99. 1889.

disappear and the naked fungous plasma, free from the infection tube, passively moves, no doubt carried by the host contents, to the vicinity of the nucleus. Here it becomes surrounded by a membrane, increases in size, and assumes an ovoid shape. In the early stages of development the host cell is not appreciably altered, but, from the figures given, presumably all or nearly all of the algal contents are eventually consumed. Details of the changes undergone by the fungous contents, which include strong vacuolization and the formation of a large central vacuole, are given by Scherffel. His account of the degrees of diplanetism exhibited by the zoospores has been mentioned in the discussion of the genus (see p. 610).

OLPIDIOPSIS FIBRILLOSA de Wildeman

La Notarisia, 10(3):34. 1895; Ann. Soc. Belge Micro. (Mém.), 20:28, pl. 2,
figs. 13-14, 18-19. 1896

(?) *Pseudolpidiopsis fibrillosa* (de Wild.) Minden, Kryptogamenfl. Mark
Brandenburg, 5:259. 1911 (1915).

Sporangium spherical or ellipsoidal; zoospores not observed; resting spore spherical or ellipsoidal, 20-25 μ in diameter (?), wall thick, densely covered with long delicate radiating fibrils, germination not observed; companion cells one or several, spherical, 12 μ in diameter, with a thin smooth colorless wall.

In *Spirogyra* sp. (coll. Massart), de Wildeman (*loc. cit.*), BELGIUM (LUXEMBOURG); *Spirogyra longata*, Domján (1936:41, pl. 1, figs. 1-2, 24, 36), HUNGARY.

The resting spores figured by Domján have much larger fibrils than those shown by de Wildeman, and one appears to lack a companion cell.

OLPIDIOPSIS APPENDICULATA de Wildeman

La Notarisia, 10(3):34. 1895; Ann. Soc. Belge Micro. (Mém.), 20:30, pl. 1,
figs. 4, 8-12. 1896

(?) *Pseudolpidiopsis appendiculata* (de Wild.) Minden, Kryptogamenfl.
Mark Brandenburg, 5:259. 1911 (1915).

Sporangium spherical or ellipsoidal, with a smooth thin colorless wall and a single short discharge tube, causing swelling of the infected

cell; zoospores not observed; resting spore spherical, 9–15 μ in diameter, thick-walled, the outer surface moderately covered with sharp spines 3–10 μ long, germination not observed; companion cell vermiciform, 20 μ long, with a thin smooth colorless wall, proximal part expanded.

In *Mesocarpus* sp., FRANCE (?) ("BELŒIL").

OLPIDIOPSIS ZOPFII de Wildeman

La Notarisia, 10 (3):34. 1895; Ann. Soc. Belge Micro. (Mém.), 20:26, pl. 1, figs. 1–3, 5–7. 1896

(?) *Pseudolpidiopsis Zopfii* (de Wild.) Minden, Kryptogamenfl. Mark Brandenburg, 5:259. 1911 (1915).

Sporangium spherical or ovoid, with a single discharge tube, wall thin, smooth, colorless, causing swelling of the infected cell; zoospores not observed; resting spore spherical, thick-walled, 16–22 μ in diameter, covered with numerous coarse sharp spines, germination not observed; companion cells from one to three, spherical, 12 μ in diameter, with a thin smooth colorless wall.

In *Spirogyra* sp., coll. Massart, BELGIUM (LUXEMBOURG).

OLPIDIOPSIS ANDREEI (Lagerheim) Sparrow

Biol. Bulletin, 70:245, text figs. 1–8, 12. 1936

Pleotrichelus Andreei Lagerheim, in Ymer, Tidskr. Svenska Sällskap. Antropol. Geogr., 19 (4):436, fig. 1. 1899.

Bicilium Andreei (Lagerheim) H. E. Petersen, Oversigt Kgl. Danske Videnskab. Selskabs. Forhandl., 1905 (5):448, fig. I, 3–6.

Pleotrichelus Ectocarpi Jokl, Oesterr. botan. Zeitschr., 66:267, pls. 4–5. 1916.

Petersenia Andreei (Lagerheim) Sparrow, loc. cit.

Sporangia from one to twenty-three in a cell, predominantly spherical, 5–39 μ in diameter, or ellipsoidal and 8–15 \times 15–25 μ , wall thin, smooth, colorless, with from one to seven cylindrical radiating discharge tubes up to 78 μ in length by 3–5 μ in diameter; zoospores irregularly pyriform, 4–5 μ long by 3 μ wide, with a refractive area at either end, anteriorly biflagellate, the flagella equal and oppositely directed, initiating movement within the sporangium and escaping by flagellar action through the open end of the discharge tubes, movement erratic; resting spore spherical or ellipsoidal, 12–23 μ in

diameter, with a thick smooth brownish wall and contents with globules; companion cell thin-walled, colorless, 4–8 μ in diameter, sometimes nearly as large as the receptive thallus.

In *Spongomorpha* sp. (coll. André), Lagerheim (*loc. cit.*), KING CHARLES LAND (Arctic); *Acrosiphonia incurva*, *Acrosiphonia* sp., *A. hystrix*, (coll. A. Jessen), Petersen (*loc. cit.*), GREENLAND; *Acrosiphonia* sp. (coll. K. Rosenvinge), *A. incurva*, Petersen (*loc. cit.*), *Ectocarpus* sp., *Striaria attenuata*, Sparrow (1934c:17, pl. 4, figs. O–S), DENMARK; *Ectocarpus granulosus*, Jokl (*loc. cit.*), "ADRIATIC"; *Ectocarpus siliculosus*, Sparrow (1936b), UNITED STATES.

Further observations are needed to confirm the sexual process preceding the formation of the resting spores. Companion cells were found in both the Danish and the American material, but, save in one specimen, only after passage of the protoplasm from the companion cell had been completed. The great variation in the size of the companion cells in the American material particularly needs further explanation.

Fragmentary observations on other "*Pleotrichelus*"-like marine forms have been reported by Sparrow (1934c, 1936b); some of these forms approximate *Olpidiopsis Andreei*. One, found in *Ceramium diaphanum*, had spherical sporangia up to 96 μ or more in diameter with ten or more radiating discharge tubes. Another completely filled the egg of a microscopic animal and formed from one to three broad discharge tubes, through which biflagellate zoospores emerged.

IMPERFECTLY KNOWN SPECIES OF OLPIDIOPSIS

? *OLPIDIOPSIS APHANOMYCIS* Cornu

Ann. Sci. Nat. Bot., V, 15:148, pl. 4, figs. 5–11. 1872

Pseudolpidium Aphanomyces (Cornu) Fischer, Rabenhorst. Kryptogamen-Fl., 1(4):37. 1892.

Sporangia spherical, solitary or in groups of three or more in terminal or intercalary swellings of the host hypha, with a single fairly broad discharge tube; zoospores and resting spore not observed.

Parasitic in *Aphanomyces* sp., FRANCE.

Two fungi with two different types of resting spores have been regarded by later investigators as belonging to this species. Dan-

geard (1890-91b:90, pl. 4, figs. 9-11) figures in *Pythium* and *Aphanomyces* a spiny spore without a companion cell, as does Butler (1907:132, pl. 9, figs. 1-7) in *Aphanomyces* alone. Petersen (1910: 539, fig. 27), on the other hand, shows one in *Aphanomyces* with a warty surface, like that of *Olpidiopsis vexans*, and bearing a companion cell. Which occurred in Cornu's fungus is, of course, not known. Of the resting stages observed, Petersen's unquestionably belongs to a species of *Olpidiopsis*, and when further observations are made on the sporangial stage Cornu's species can then be redefined. Petersen suggests that his fungus may be identical with *O. vexans* and that the smaller size is due to poor conditions of nourishment within the host. The observations of the various investigators since Cornu may be summarized as follows:

Sporangia spherical or ellipsoidal, from one to six, lying loosely in intercalary and terminal swellings of the host hypha, wall thin, smooth, colorless, with from one to two discharge tubes; zoospores somewhat ovoid, flattened, with two laterally attached flagella, upon escape soon coming to rest in a group, assuming motility after from four to five minutes, and dispersing; resting spore spherical, with a thin or somewhat thickened (brownish?) wall covered with short spines or warts, with or without a companion cell.

Parasitic in hyphae of *Aphanomyces sp.*, Dangeard (*loc. cit.*), FRANCE; Butler (*loc. cit.*), INDIA; Minden (1915:267), GERMANY; Petersen (*loc. cit.*), DENMARK.

? *OLPIDIOPSIS ELLIPTICA* (Schroeter) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):41. 1892

Diplophysa elliptica Schroeter, in Cohn, Kryptogamenfl. Schlesien, 3(1):196. 1885.

Resting spore transversely ellipsoidal, occupying nearly the whole breadth of the host cell, with light-brown wall covered with delicate spines; companion cell slightly smaller than the resting spore, with a smooth brown wall; sporangium and zoospores not observed.

In *Mesocarpus sp.*, GERMANY.

? OLPIDIOPSIS SOROKINEI de Wildeman

Ann. Soc. Belge Micro. (Mém.), 14:22, fig. 7. 1890

Olpidium Sorokinei de Wildeman, Bull. Soc. Roy. Bot. Belg. (Mém.), 35:16. 1896.

This fungus, known only in the sporangial stage, was separated from *Olpidiopsis Oedogoniarum* because it occurred in *Tribonema bombycinum* in Belgium and did not infect filaments of *Oedogonium* in the same lot of material. The flagellation of the zoospores was not observed. A similar fungus has been found in Michigan in the same host. Resting spores with companion cells were formed, but the sporangia were empty, and hence the flagellation of the zoospores could not be determined. If conclusive experimental evidence is given in the future with regard to host specificity the species should be maintained as distinct from *O. Oedogoniarum*. (See also p. 103.)

? OLPIDIOPSIS SPHACELLARUM (Kny), comb. nov.

Chytridium (Olpidium) Sphacellarum Kny, Sitzungsber. Gesell. Naturforsch. Freunde Berlin, 1871:97; Hedwigia, 11(6):87. 1872.

Pleotrichelus Sphacellarum (Kny) H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905:452, fig. II, 5-8.

Sporangia single or up to nine in a cell, frequently attacking the terminal or other cells of the lateral branches and occasionally the apical cell of the main axis, as well as the setae, causing swelling of the infected cell, spherical, subspherical, or oblong, variable in size, 35-45 μ long by 17-52 μ in diameter, wall thin, smooth, colorless, bearing from one to three short stout discharge tubes 8-10 μ in diameter; zoospores somewhat pyriform, 4 μ long by 2 μ in diameter, with a posterior colorless granule and two oppositely directed flagella, initiating movement within the sporangium and emerging rapidly through the dissolved tip of the discharge tube, movement even, with sudden stops and changes of direction; resting spore not observed.

Parasitic in cells of *Cladostephus spongiosus*, Kny (*loc. cit.*), WALES; *Cladostephus spongiosus*, Magnus (1875:77, pl. 1, figs. 17-20), HELGOLAND; *Sphacelaria tribuloides*, Pringsheim (1855:153, fig. 25), ITALY; *Sphacelaria cirrhosa*, Magnus (*loc. cit.*), *Chaetopteris plumosa*, Petersen (1905:452, fig. II, 5-8), DENMARK; *Sphacelaria cirrhosa*,

Sparrow (1936b:250, text figs. 9-11, pl. 1, fig. 3, pl. 2, fig. 5), UNITED STATES.

Pringsheim, who considered the fungus to be the antheridium of the alga, shows the zoospores—probably correctly—to be biflagellate. Though the exact generic disposition of this species must await the discovery of the resting stage, it appears, from what is known of it now, more closely related to *Olpidiopsis* than to *Olpidium*, *Chytridium*, or *Pleotrichelus*.

Observations on the American material indicate that the zoospore effects penetration of the cell by means of a tube through which the contents pass. The young thallus often very quickly attaches itself to the nucleus of the host. When cells of the lateral branches are attacked they soon exhibit pronounced swelling. The fungus was a true parasite, invading only the healthy host cells and accomplishing alone the disintegration of the contents. No further spread of the infection was noted after the alga had been kept even for a short time under laboratory conditions.

EXCLUDED SPECIES OF OLPIDIOPSIS

* *OLPIDIOPSIS LONGICOLLIS* Zopf, nom. nudum

Schenk, Handbuch d. Bot. . . . , 4:508. 1890

This name was applied to an incompletely observed parasite in the zoocyst of *Vampyrella Spirogyrae* figured by Zopf (1888:351, pl. 19, fig. 14).

PETERSENIA SPARROW

Dansk Bot. Ark., 8(6):13. 1934

(Figure 58 H, p. 619; Figure 59 C-I, p. 633)

Pleotrichelus sectio lobati H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905:460.

Thallus appearing at first somewhat plasmodial, at maturity lobed, contorted, or tubular, rarely ellipsoidal and unlobed, holocarpic, without a specialized vegetative system; sporangium with from two to several discharge tubes (rarely one); zoospores biflagellate, monoplanetic, formed within the sporangium, where they assume motility, escaping individually through pores at the apex of the discharge tubes; resting spore not observed.

Primarily parasitic or saprophytic in marine algae; one species (*Petersenia irregularis*) parasitic in the hyphae of fresh-water aquatic Phycomycetes.

In the method of the formation of the zoospores, as well as in their shape and flagellation, *Petersenia* strongly resembles *Olpidiopsis*. The irregular lobed or tubular character of the mature thallus, however, and, to a lesser degree, the formation typically of more than one discharge tube distinguish it.

As understood here, *Petersenia* includes only forms with irregular tubular or lobed thalli. The species with more regular spherical or ellipsoidal sporangia also found in marine algae (*Pleotrichelus sectio integri* H. E. Petersen, *op. cit.*, p. 448) are considered too closely allied to *Olpidiopsis* to be segregated generically. They differ so far as is known from members of *Olpidiopsis* only in their marine habitat and in being generally provided with more than one discharge tube. Further work may, however, reveal that they have distinguishing characters of more significant taxonomic worth.

In both of the marine species the thalli are predominantly lobed under optimum conditions for development. When the plant is crowded or when nutrient is not readily available lobation may be less pronounced or even absent, in which case an "olpidioid" type of thallus and sporangium may be formed.

KEY TO THE SPECIES OF PETERSENIA

- In marine algae; thallus elongate and lobed or consisting of a complex of lobulations
Thallus predominantly elongate, strongly lobed *P. lobata*, p. 631
Thallus consisting of a complex of strongly inflated broadly pyriform closely interlocked lobes *P. pollagaster*, p. 632
In hyphae of fresh-water filamentous Phycomycetes; thallus tubular, branched *P. irregularis*, p. 634

PETERSENIA LOBATA (H. E. Petersen) Sparrow

Dansk Bot. Ark., 8(6):13, pl. 2, figs. I-N. 1934

(Figure 59 D-I, p. 633)

Pleotrichelus lobatus H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905:460, fig. V, 1-7.

Sporangium elongate, somewhat cylindrical, with lobes of various sizes, particularly near the extremities, sometimes ellipsoidal and

unlobed, 30–192 μ long by 15–30 μ in width, at times extending through several cells of the alga, with from one to three discharge tubes of varying length; zoospores pyriform, 4.5 μ long by 3 μ in width, with a refractive anterior globule and two anteriorly attached oppositely directed flagella; resting spore not observed.

Weakly parasitic or saprophytic in *Callithamnion corymbosum* (coll. K. Rosenvinge), *C. Hookeri*, *Spermothamnion Turneri*, Petersen (*loc. cit.*), *S. repens* var. *Turneri*, Sparrow (*loc. cit.*), DENMARK; *Callithamnion roseum*, Sparrow (1936b:245, pl. 2, figs. 1–2), UNITED STATES.

Observations on zoospore production in this species (Sparrow, 1934c) showed that the swarmers were fully formed within the sporangium by a process of cleavage, which resembled in its later stages that found in the vesicle of *Pythium*. The spore initials gradually assumed an individual rocking movement, which became more pronounced as separation and fashioning of the spores proceeded. Around the periphery of the spore mass, which at this stage did not completely fill the sporangium, traces of flagellar movement became visible. In later stages the flagella became very apparent, being laterally attached to the shallow-grooved zoospores. These escaped individually, by their own motility, through the discharge tubes.

PETERSENIA POLLAGASTER (H. E. Petersen) Sparrow

Dansk Bot. Ark., 8 (6):15, pl. 3, figs. I–K. 1934

(Figure 59 C)

Pleotrichelus pollagaster H. E. Petersen, Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905:462, fig. VI, 1–5.

Sporangium consisting of a complex of strongly inflated broadly pyriform lobulations, rarely only slightly lobed, large specimens 112 \times 104 μ , small ones 35 \times 43 μ , with from one to four cylindrical discharge tubes of variable length (10–100 μ); zoospores biflagellate, presumably issuing through the discharge tubes; resting spore not (?) observed.

In *Ceramium rubrum*, H. E. Petersen (*loc. cit.*), *Ceramium* sp., Sparrow (*loc. cit.*), DENMARK.

The characteristic complex of lobulations in well-developed specimens is striking, and cannot be confused with the more open type found in *Petersenia lobata*.

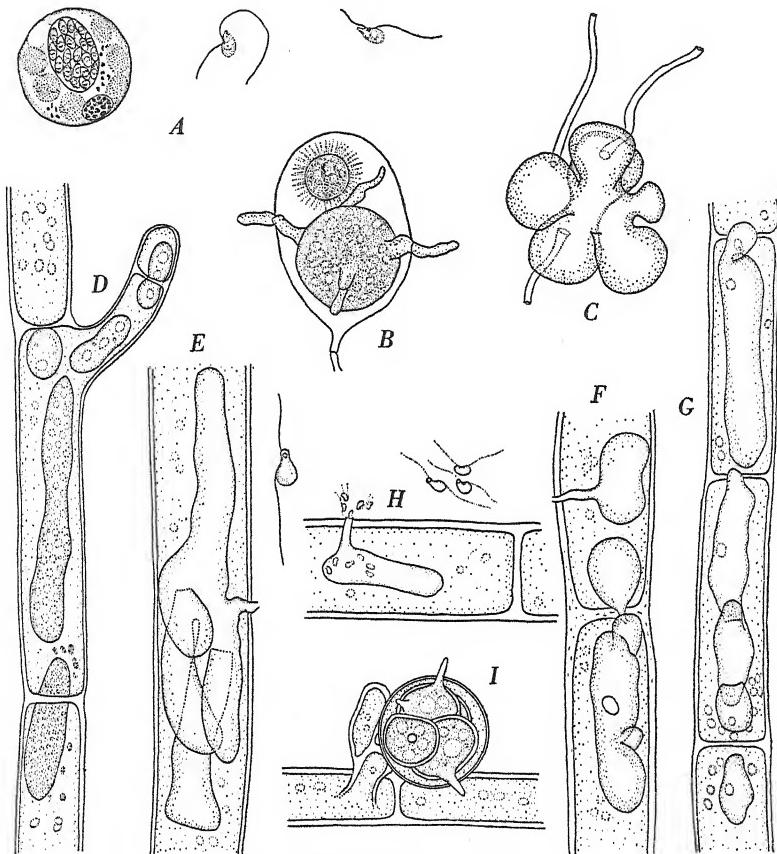


FIG. 59. Olpidiopsidaceae

A. Pseudosphaerita Euglena Dangeard in *Euglena*, parasitized host containing mature sporangium; to the right are two zoospores, enlarged, showing their biflagellate nature. *B. Pseudolpidium gracile* E. J. Butler ($\times 300$) on *Pythium intermedium*, mature sporangium, with four discharge tubes and a resting spore, within hypertrophied part of host. *C. Petersenia pollagaster* (Petersen) Sparrow ($\times 500$), empty sporangium with three discharge tubes. *D-I. Petersenia lobata* (Petersen) Sparrow in the red seaweed *Spermothamnion*: *D*, portion of frond of host showing thalli of fungus in various stages of development ($\times 250$); *E-G*, empty sporangia within host showing various types of lobulations ($\times 250$); *H*, discharging zoosporangium (zoospore at left is a freehand enlargement; those at right are $\times 500$); *I*, tetraspores of host containing nearly mature sporangia of parasite ($\times 250$).

(*A*, Dangeard, 1933; *B*, Butler, 1907; *C-I*, Sparrow, 1934c)

Thick-walled resting structures occupying all or part of the lobed thallus have been found by Petersen (see Sparrow, *op. cit.*, pl. 3, figs. I, K). Whether they belong to the fungus or are cysts of extraneous parasitic organisms has not been determined.

PETERSENIA IRREGULARE (Constantineanu), comb. nov.

(Figure 58 H, p. 619)

Olpidiopsis irregularis Constantineanu, Revue Gén. Bot., 13:373, figs. 76 A-K, 77. 1901.

Sporangium predominantly irregularly tubular, with short contorted branches or lobes of varying length, occasionally ellipsoidal or narrowly reniform, the whole complex 40-90 μ long, causing pronounced swelling of the infected part (generally the apex) of the hypha, with a single short sessile or slightly protruding discharge tube; zoospores somewhat reniform, 4.5-5 μ long by 3-4.5 μ wide, with a few granulations or a small droplet and two unequal oppositely directed flagella, the anterior one shorter than the posterior, emerging quickly in a group or individually through the orifice of the discharge tube, movement slow and even; resting spore not observed.

Parasitic in hyphae of *Saprolegnia sp.*, Constantineanu (*loc. cit.*), RUMANIA; *Achlya sp.*, Sparrow (1934c:15), DENMARK.

Minden (1915:264) considered the species a doubtful member of *Olpidiopsis*, since no resting stage was observed. Observations on this phase of the present species as well as on *Petersenia lobata* and *P. pollagaster* may result in its segregation from *Petersenia* as well.

PYTHIELLA COUCH

Mycologia, 27:160. 1935

(Figure 58 G, I, p. 619)

"Plant body parasitic within the threads of *Pythium*; without rhizoids, the entire thallus upon maturity being transformed into reproductive organs. Spore development as in the higher water fungi (*Achlya* and *Saprolegnia*, e.g.). Spores after emergence encysting at the tip of the sporangium as in *Achlya*, swarming later in the laterally biciliate condition. Antheridia present on all oogonia. Egg not completely filling the oogonium, and with distinct periplasm" (Couch, *loc. cit.*).

An endobiotic holocarpic parasite in the hyphae of algae-inhabiting species of *Pythium*.

The genus is of great interest in view of the simpler organization found in *Olpidiopsis*. In the latter the zoospores exhibit no well-defined diplanetism, and the sex organs are less highly specialized. For example, the protoplasm of the contributing thallus in *Olpidiopsis* is conveyed into the receptive structure through a pore. The resting-spore wall is composed in part, at least, of the wall of the receptive thallus, and there is no differentiation at maturity (except in *O. Oedogoniarum*) between the spore and its container. In *Pythiella*, on the other hand, there is a well-defined diplanetism of the zoospores (Fig. 58 G), a fertilization tube is formed by the contributing thallus (Fig. 58 I), and the protoplasm of the receptive thallus is differentiated into periplasm and oöplasm. At maturity the resting spore has a distinct wall of its own and lies loosely in its container.

Because of the similarity in the sequence of protoplasmic changes preceding zoospore formation in *Pythiella* to that found in *Ectrogella*, where strong vacuolization, "balling," and homogeneous and segmented stages occur, Couch concludes that the two genera are closely related.

PYTHIELLA VERNALIS Couch

Mycologia, 27:160, figs. 1-27. 1935

"Sporangia developing in the threads of *Pythium*, spherical or rarely subspherical when mature, without mycelium and rhizoids; causing the formation of a distinct gall in the *Pythium* thread, usually one sporangium in each gall though two, three or four may not uncommonly occur; 10-30 μ thick, emptying through a long tube up to 50 μ long and about 4 μ thick; on some sporangia several tubes may be formed (as many as five), some of which may be branched. Spores diplanetic, encysting after discharge, at the tip of the sporangial tube, emerging from the cysts after about an hour, elongated with a longitudinal groove and with two cilia; spores 3.7-4 μ thick. In swimming the active cilium is directed forward while the posterior one is dragged along behind. Sexual reproduction is by oogonia and antheridia; oogonia 11-18.5 μ thick, spherical, containing one egg, which does not completely fill the oogonium; eggs 9-15 μ thick, spherical, when mature surrounded by a thick wall and a small amount of periplasm;

antheridium spherical, about 5μ thick, emptying its entire contents through a delicate tube into the egg" (Couch, *loc. cit.*).

Parasitic in the hyphae of *Pythium gracile* and *P. dictyosporum*, UNITED STATES.

PSEUDOLPIDIUM A. FISCHER

Rabenhorst. Kryptogamen-Fl., 1(4):33. 1892

(Figure 59 B, p. 633)

Olpidiopsis sensu Fischer, Jahrb. wiss. Bot., 13:363. 1882. Non Cornu.

Thallus endobiotic, holocarpic, without a specialized vegetative system, at first naked and somewhat amoeboid, later walled, predominantly spherical or ellipsoidal, forming the rudiment of the sporangium or resting spore; sporangium smooth-walled, with from one to several discharge tubes, zoospores laterally biflagellate, produced in the sporangium; resting spore somewhat thick-walled.

Parasitic in Pythiaceae.

The present status of this genus has been previously discussed (see p. 609).

KEY TO THE SPECIES OF PSEUDOLPIDIUM

- Resting spore spherical, the yellowish wall covered with long tenuous spines *Ps. gracile*, p. 636
- Resting spore ovoid, the brown wall covered with delicate evenly placed short spines *Ps. Pythii*, p. 637

PSEUDOLPIDIUM GRACILE Butler

Mem. Dept. Agr. India, Bot. Ser., 1:131, pl. 7, figs. 1-8. 1907

(Figure 59 B, p. 633)

"Sporangia single or multiple, formed in swollen diverticula of the hyphae of the host, spherical, up to 52μ in diameter, with a single or more usually several, rather long, tubes, opening to the exterior; zoospores as in other members of the genus; durable spores spherical, yellowish, rather thin-walled, with long tapering spines thickly crowded; germination not observed" (Butler, *loc. cit.*).

Parasitic in *Pythium intermedium*, FRANCE.

Infected terminal and lateral branches formed large (up to 80–90 μ long) ovoid or balloon-shaped swellings, in which as many as forty sporangia were produced.

PSEUDOLPIDIUM PYTHII Butler

Mem. Dept. Agr. India, Bot. Ser., 1:129, pl. 7, figs. 9–16. 1907

"Sporangia single or multiple, formed in swollen diverticula of the hypha of the host, oval, 35 μ in longer diameter, with a single tube opening to the outside and variable in length; zoospores elongated, unequilateral, with two flagella, one from the narrow end in front, and the other lateral near the back; durable spores numerous, single, or with sporangia or other durable spores, oval or spherical, 19–30 μ in diameter, wall brown, rather thin, provided with fine, short, evenly spaced spines; germination not observed" (Butler, *loc. cit.*).

Parasitic in *Pythium monospermum*, *P. rostratum*, *P. vexans*, and *P. intermedium*, Butler (*loc. cit.*), FRANCE; (?) *Pythium sp.*, Minden (1915:268), GERMANY; *Pythium Oryzae*, Tokunaga (1933a:22, pl. 2, figs. 3–4), JAPAN; (?) *Pythium spp.*, Sparrow (1936a:425), ENGLAND.

Neither Minden nor Sparrow is certain of his identifications. No zoospores were observed in the British material. The fungus occurring on *Pythium* but included by Dangeard (1890–91b:90) under *Olpidiopsis Aphanomyces* may be referable to this species.

IMPERFECTLY KNOWN SPECIES OF PSEUDOLPIDIUM

? PSEUDOLPIDIUM DEFORMANS Serbinow

Scripta Bot. Horti Univ. Imper. Petro., 24:154, pl. 1, figs. 1–12, pl. 4, figs. 16–28. 1907

Thallus at first naked, amoeboid, dividing into several parts; sporangium spherical, up to 35 μ in diameter, or long-ovoid, 30.5–47.5 μ long by 14.5–27 μ wide, from one to eleven in the swollen host cell, discharge tube cylindrical, up to 15.8 μ long by 8 μ in diameter; zoospores spherical or ovoid, 3.2–4.8 μ in diameter, with two laterally attached flagella, strongly metabolic (amoeboid?), without (?) an oil droplet, swimming away immediately after discharge.

Parasitic in lateral branch cells of *Draparnaldia glomerata*, RUSSIA.

Although strongly resembling a species of *Pseudolpidium* or *Olpidiopsis* this fungus differs in the fragmentation of the thallus. It is possible that Serbinow confused multiple infection with fragmentation. The figures given afford evidence for both interpretations. The zoospores are said to be without an oil droplet, but this structure is clearly shown in the figures.

? *PSEUDOLPIDIUM GLENODINIANUM* (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):36. 1892

Olpidium Glenodinianum Dangeard, Journ. de Botanique, 2:131, pl. 5, figs. 6-10. 1888.

Sporangium spherical or ellipsoidal, wall thin, smooth, colorless, discharge tube a more or less elongate papilla which pierces the host wall; zoospores about one hundred, spherical, sometimes elongate, laterally biflagellate, with a single globule, discharged in a mass imbedded in mucus and forming for a few seconds a group at the orifice; resting spore not observed.

Parasitic in *Glenodinium cinctum*, FRANCE.

? *PSEUDOLPIDIUM SPAERITAE* (Dang.) Fischer

Rabenhorst. Kryptogamen-Fl., 1(4):36. 1892

Olpidium Sphaeritae Dangeard, Le Botaniste, 1:51, pl. 3, figs. 3-7. 1889.

Sporangium ovoid to somewhat pyriform, wall thin, smooth, colorless, with a long discharge tube which pierces the wall of the cyst; zoospores ellipsoidal, laterally biflagellate; resting spore not observed.

In spiny and smooth resting spores of *Sphaerita endogena*, Dangeard (*loc. cit.*), FRANCE.

PSEUDOSPHERITA DANGEARD

Le Botaniste, 4:242. 1894-95

(Figure 59 A, p. 633)

Thallus endobiotic, holocarpic, contents vacuolate during maturity; sporangium without a discharge tube; zoospores biflagellate,

the flagella attached subapically, the shorter directed anteriorly, the longer posteriorly, formed by successive divisions of the contents, escaping by fracturing of the wall.

Parasitic in the cytoplasm of *Euglena*, *Cryptomonas*.

Pseudosphaerita Dangeard is apparently related to *Olpidiopsis* and *Pseudolpidium*. Observations on the method of formation of the resting spore will be necessary, however, to determine its precise affinities.

The genus was founded by Dangeard to include *Sphaerita*-like forms with biflagellate zoospores. Although the thallus superficially resembles that of *Sphaerita*, Dangeard (1933) has pointed out that the two fungi may be distinguished by the different methods of zoospore formation. In *Sphaerita* this is simultaneous. In *Pseudosphaerita* each division of the nucleus of the thallus is followed by a division of the cytoplasm. No mitotic figures were observed. At maturity the contents are cleaved into from 64 to 128 polygonal uninucleated segments. These become flagellate zoospores and may swarm a long time within the sporangium before being liberated. Occasionally, they are discharged within the host and undergo germination *in situ*. The nucleus of these zoospores is larger (2.5μ) than that formed in the swarmer of *Sphaerita* and possesses a more or less central nucleolus. Although the method of zoospore formation in *Pseudosphaerita* is unusual and has led Dangeard (*loc. cit.*) to suggest the erection of a separate family for the inclusion of similar forms with a successive type of spore maturation, it is not unique and has also been observed in true chytrids.

The parasite may develop and sporulate within the moving host or may attack resting individuals. Puymaly (1927), however, observed that *Euglena viridis* attacked by a fungus called by him *Sphaerita*, but with biflagellate zoospores and hence probably *Pseudosphaerita*, quickly ceased its flagellar action after infection. It continued to show signs of life until sporulation of the fungus occurred. He also noted that the zoospores of the fungus were strongly attracted to the *Euglena*. The method of infection, however, was not determined. Puymaly, recalling the conjecture of sexuality in *Sphaerita* proposed by Chatton and Brodsky (1909) and based on observations of conjugation in a *Sphaerita*-like organism by Doflein

(1907), was certain that in his fungus the biflagellate swarmers were zoospores and not zygotes.

KEY TO THE SPECIES OF PSEUDOSPHAERITA

- Parasitic in *Euglena*; globules of zoospores not radiately arranged in the sporangium *Ps. Euglenae*, p. 640
Parasitic in *Cryptomonas*; globules of zoospores radiately arranged in the sporangium *Ps. radiata*, p. 640

PSEUDOSPHAERITA EUGLENAE Dangeard

Le Botaniste, 4:242, fig. 9. 1894-95; *ibid.*, 25:36, pl. 4, figs. 3-15. 1933
(Figure 59 A, p. 633)

Sporangium somewhat ellipsoidal, oblong, or tubular; zoospores elongate-pyriform with attenuated apex, 6 μ long by 2.5-3 μ wide, with a small granule at the point of insertion of the flagella, initiating movement within the sporangium, swimming motion accompanied by a trembling of the body.

Parasitic in the cytoplasm of *Euglena*, sometimes accompanying *Sphaerita*, FRANCE.

PSEUDOSPHAERITA RADIATA (Dang.), comb. nov.

Sphaerita radiata Dangeard, Le Botaniste, 2:54, pl. 2, fig. 20. 1890-91.

From one to three parasites in the host, variable in position, if one, occurring at the rear of the body, near the nucleus of the host, the host cell becoming completely deformed and its contents being disorganized as the parasite matures; at maturity the globules of the zoospores showing a distinct radiate arrangement in the sporangium, the latter upon the rupture of the host wall being projected from the host cell, the freed biflagellate zoospores becoming narrow at their two extremities and taking the form of a small rod with a globule in the center; resting spore not observed.

In *Cryptomonas*, FRANCE.

IMPERFECTLY KNOWN GENUS OF THE OLPIIDIOPSISIDACEAE

? BLASTULIDIOPSIS Sigot

C. R. Soc. Biol. (Strasbourg), 108:34, 3 figs. 1931

? BLASTULIDIOPSIS CHATTONI Sigot

Loc. cit.

Zoospore upon coming to rest on the host cell losing its flagella and producing a tube that penetrates the host wall and forms within the host a short filament, which enlarges, expands, and branches, the branches forming broad lobes of varying size, the whole thallus transformed at maturity into a single sporangium; zoospores 6-8 μ (long?) with two laterally attached opposed flagella, 15-20 μ in length, and an anterior globule, formed within the sporangium, where individual movement is initiated, and escaping through a pore at the tip of a short discharge tube; resting spore not observed.

Parasitic in eggs of *Cyclops* (fresh-water crustacean), FRANCE.

The thallus is said to be plasmodial and unwalled until just before formation of the zoospores. In the course of development large vacuoles appear in the cytoplasm, which fuse to form one large vacuole. The nuclei at maturity are distributed regularly in the cytoplasm surrounding the central vacuole; the spores are cleaved out simultaneously (synchronously) around each of the nuclei.

In the method of formation of the zoospores, their activity within the sporangium, their manner of discharge, and their structure *Blastulidiopsis* resembles *Olpidiopsis*. Its zoospores are, however, much larger. The lobed nature of the sporangium constitutes a strong resemblance to *Petersenia*.

The method whereby the zoospore reaches the eggs still within the egg sac of the animal is not given by Sigot.

He noted that the period of time necessary from infection to sporulation of the parasite was about equal to the time between fertilization and the occurrence of the *Nauplius* stage of the host. The disease appeared in late February or early March and disappeared during May.

The form is difficult to typify because the observations have in the main been derived from sectioned and stained material. Further work of a purely morphological nature is necessary in order clearly to characterize the genus.

SIROLPIDIACEAE

Thallus endobiotic, holocarpic, without a specialized vegetative system, unbranched or with rudimentary branches, at maturity typically forming a linear series of sporangia, walls giving a cellulose reaction, contents undergoing strong vacuolization; sporangia with a single discharge tube (occasionally several); zoospores biflagellate, monoplanetic, formed in the sporangium; resting stage unknown.

So far as is known, an exclusively marine group, parasitic and saprophytic in green and red seaweeds.

The thallus, although more highly developed than that of the Olpidiopsidaceae, is, under natural conditions, very rudimentary in character. In both *Sirolpidium* and *Pontisma* the mature thallus may consist of no more than a single cell, and then it strongly resembles *Olpidiopsis*. Typically, however, a linear septate type is formed which parallels that found in the chytrid *Septolpidium*.

KEY TO THE GENERA OF THE SIROLPIDIACEAE

- Thallus typically narrowly tubular, at maturity becoming septate,
the fragments disarticulating SIROLPIDIUM, p. 642
- Thallus broadly tubular, often with short, irregular branches, not
disarticulating PONTISMA, p. 645

SIROLPIDIUM H. E. PETERSEN

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):480
(Figure 60, p. 644)

Thallus endobiotic, holocarpic, without specialized vegetative structures, consisting either of a simple saclike body formed directly from an expanded endobiotic zoospore or more commonly of an unbranched or occasionally branched hypha-like tube, contents at first vacuolate, later with numerous refractive granules; sporangium

formed from the saclike body or from fragments of the linearly septate progressively disassociated tube, provided with a single discharge tube, the tip of which at least is ordinarily extramatrical; zoospores fully formed within the sporangium, where movement is initiated, grape-seed-like, with a small refractive anterior granule and two anteriorly attached oppositely directed flagella, swimming individually through a pore formed at the tip of the discharge tube; resting stage not observed.

The genus, so far as is known, is confined to marine green algae.

The fungus on which the genus is based is distinct, as Petersen pointed out, from all other related forms in the peculiar septation and subsequent disassociation of the tubular thallus. In very early stages the thallus is a somewhat irregular, curved cylindrical structure just within the host wall (Fig. 60 A). As it matures it elongates and becomes progressively separated by cross walls into a linear series of spherical or cylindrical segments of varying size, each of which becomes an independent walled unit (Fig. 60 E, G). In many such chains the wall of the original thallus can be detected between the segments (Fig. 60 G). Each of the fragments assumes individual growth, soon loses its original orientation with respect to the "parent" thallus, and ultimately becomes a single sporangium with a discharge tube (Fig. 60 B-D, H). Often when the latter structures are not orientated so as to pierce the algal wall they attain great lengths and bear a striking resemblance to the hyphae of a filamentous phycomycete (Fig. 60 F). In this connection it has been observed (Sparrow, 1936b:254) that fragments of the thallus permitted to develop in close contact with the atmosphere, by allowing sea water to drip over them rather than by submerging them, for example, underwent a remarkable transformation in body structure. Instead of being somewhat olpidioid or moniliform they became extensive isodiametric tubular structures which simulated in every respect, as did the discharge tubes, the hyphae of higher Phycomyces. Because of these facts it is obvious that *Sirolpodium* is of very definite interest in the problem of the origin of the mycelium in the biflagellate series of Phycomycetes. The zoospores are grape-seed-like and biflagellate (Fig. 60 I).

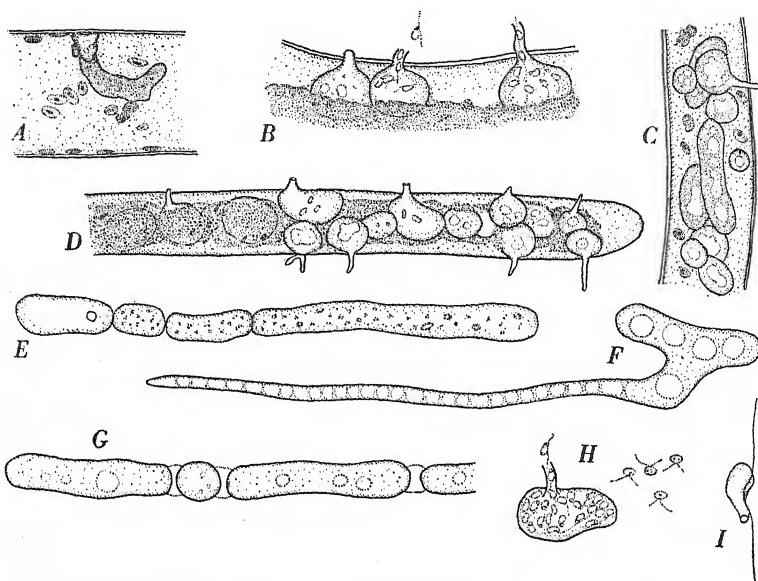


FIG. 60. *Sirolpodium Bryopsidis* (de Bruyne) H. E. Petersen

A. Portion of filament of *Bryopsis* showing an early stage in development of fragmenting type of thallus ($\times 320$). B. Olpidioid sporangia discharging their zoospores ($\times 580$). C. Fragmenting thallus each part of which becomes a single sporangium ($\times 320$). D. Tip of filament of *Bryopsis* showing a group of olpidioid sporangia ($\times 320$). E. Thallus fragmenting ($\times 580$); cell at extreme left has already discharged its zoospores. F. Long discharge tube produced by thallus ($\times 580$). G. Thallus fragmenting ($\times 580$); traces of original thallus wall are seen connecting the parts. H. An olpidioid sporangium discharging its zoospores ($\times 580$), and, at right, zoospores which were killed with osmic acid and stained with fuchsin to show flagella ($\times 766$). I. Interpretation of zoospore (enlarged, freehand drawing).

(Sparrow, 1934c)

SIROLPIDIUM BRYOPSIDIS (de Bruyne) H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):480, fig. 9.

Olpidium Bryopsidis de Bruyne, Arch. de Biol., 10:85, pl. 5, figs. 1-15.
1890.

Disarticulated sporangia, $8-90 \mu$ long by $7-16 \mu$ in diameter, olpidioid types $18-38 \mu$ in height by $12-17 \mu$ in diameter, wall thin,

smooth, colorless, discharge tube narrowly cylindrical, up to 165μ or more in length, extending for variable distances outside the alga; zoospores narrowly pyriform, somewhat arched, about 4μ long by 2μ wide, the narrow anterior end bearing a refractive granule and two oppositely directed flagella; resting spore not observed with certainty.

Parasitic or saprophytic in *Bryopsis plumosa*, de Bruyne (*loc. cit.*), ITALY; Petersen (*loc. cit.*), Sparrow (1934c:11, pl. 2, figs. A-H), DENMARK; *Bryopsis plumosa*, *Cladophora sp.*, Sparrow (1936b:252, pl. 1, figs. 4, 7, pl. 3, fig. 1), UNITED STATES.

In the American material infected plants of *Bryopsis* were recognizable macroscopically by the presence of blackened areas along the fronds. The fungus was cultivated to a small extent in dextrose solutions. In 0.5 and 1.0 per cent solutions in sea water extramatrical hyphae up to 112μ in length were obtained in forty-eight hours. Attempts to grow the fungus on solid media, however, were uniformly unsuccessful. Because of the capacity of *Siroplodium* to produce a hypha-like growth it appears to be the marine phycomycete (excluding *Pythium marinum*) best suited to cultivation.

Resting spores have not as yet been convincingly demonstrated, although de Bruyne figures spherical or ellipsoidal "cysts de conservation" and Petersen has found thick-walled bodies associated with the sporangia.

PONTISMA H. E. PETERSEN

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):482

(Figure 61, p. 646)

Thallus endobiotic, holocarpic, without specialized vegetative structures, consisting of an unbranched or irregularly branched tube of small extent, which at maturity becomes segmented, the segments few in number, occasionally oloidoid or tubular and nonseptate, contents at first vacuolate, later with numerous refractive granules, walls giving a cellulose reaction; sporangia formed from the segments, each bearing a single discharge tube (sometimes several), the tip of which, at least, is extramatrical; zoospores minute, pyriform, with a refractive body at either end and two oppositely directed flagella, completely formed within the sporangium, where motility is initiated,

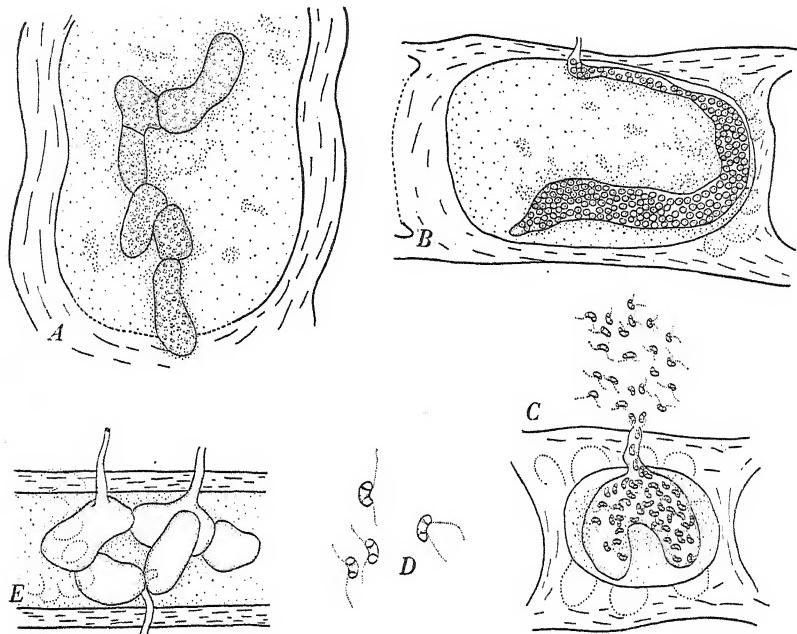


FIG. 61. *Pontisma lagenidioides* H. E. Petersen in *Ceramium*

A. Typical segmented thallus. B. Curved unsegmented sporangium within which zoospores have become quiescent. C. Discharge of zoospores from an unsegmented sporangium. D. Zoospores. E. Group of empty sporangia, all segmented portions of single thallus. (A-C, E, $\times 235$; D, $\times 575$.) (Sparrow, 1934c)

swimming individually through a pore at the tip of the discharge tube; resting stage not observed.

In *Ceramium spp.*

The genus resembles *Sirolopidium* in the segmentation of the thallus, but differs in being branched and in not exhibiting fragmentation.

Pontisma, so far as is known, occurs exclusively in the marine alga *Ceramium*. The thallus is difficult to characterize precisely because of its "generalized" aspect. Penetration of the zoospore and the very early stages in the establishment of the thallus have not been observed.

PONTISMA LAGENIDIOIDES H. E. Petersen

Oversigt Kgl. Danske Vidensk. Selskabs. Forhandl., 1905 (5):482,
fig. X, 1-3

Thallus at maturity ordinarily composed of a linear series of somewhat irregularly cylindrical simple or short-branched segments 20–60 μ long by 11–30 μ in diameter, slightly constricted or sometimes almost disarticulated at the narrow cross walls, olpidioid thalli 14–16 μ long by 13–15 μ high and tubular nonseptate thalli 130–200 μ long occasionally produced; sporangia generally forming a single narrowly cylindrical slightly tapering discharge tube (sometimes several) of variable length (up to 145 μ), the tip of which, at least, is extramatrical; zoospores numerous, somewhat bent, rod-shaped, or pyriform, 2.5–3 μ in diameter by 4.5–7 μ in length, with a strongly refractive region at either end and two short laterally attached oppositely directed flagella, swarming within the sporangium before emerging by flagellar action through the discharge tube, movement erratic, tumbling; resting spore not observed.

Weakly parasitic or saprophytic in *Ceramium rubrum*, *C. strictum*, *C. fruticosum*, Petersen (*loc. cit.*), Sparrow (1934c:11, pl. 3, figs. A–H), DENMARK; saprophytic in *Ceramium diaphanum*, Sparrow (1936b:252, pl. 1, fig. 5), UNITED STATES.

Pontisma lagenidioides, which appears to occur most commonly in the more delicate species of *Ceramium*, thrives best when the alga is kept under unfavorable environmental conditions or when it is dead.

The zoospores of this fungus closely resemble those figured by Butler (1907) for "Pleolpidium inflatum Butler," a parasite of *Pythium*.

LAGENIDIACEAE

Thallus endobiotic, holocarpic, monophagous or sometimes polyphagous, uni- or multicellular, branched or unbranched, the contents usually with a lustrous matrix within which are irregularly shaped refractive clods and globules, walls giving a cellulose reaction, the cyst of the zoospore and the infection tube frequently persistent, converted at maturity into reproductive organs; zoosporangia each

forming a single tube, through which the uncleaved or partly cleaved contents are liberated into an extramatrical more or less evanescent vesicle where maturation of the zoospores is completed; zoospores (always?) of the secondary laterally biflagellate type, with a single swarm period; sexual organs monoecious or dioecious, consisting of undifferentiated or somewhat specialized vegetative cells, periplasm apparently lacking, fertilization tube sometimes produced; oöspore thick-walled, with a large reserve globule, formed singly in the female gametangium, which it almost always nearly fills.

Parasites of fresh-water algae, primarily Conjugatae, of microscopic animals, and, in one genus (*Lagena*), of the roots of cereals and wild grasses.

KEY TO THE GENERA OF THE LAGENIDIACEAE

- [Thallus one-celled, attached to the inner host wall by a thick collar of callus; parasitic in roots of cereals *LAGENA*¹]
- Thallus uni- or multicellular, lying free in the host cell or adherent to the persistent penetration tube; parasites of algae and microscopic animals
- Thallus unbranched, monophagous, strongly constricted at the cross walls, segments regular, appearing linklike; antheridial cell poorly differentiated *MYZOCYTIUM*, p. 648
- Thallus unbranched or branched, mono- or polyphagous, little or not at all constricted at the cross walls, segments often irregular; antheridial cell usually well differentiated
..... *LAGENIDIUM*, p. 656

MYZOCYTIUM SCHENK

Ueber das Vorkommen contractiler Zellen im Pflanzenreiche, p. 10.

Würzburg, 1858

(Figure 62 A-C, F-H, p. 651)

Thallus endobiotic, tubular, unbranched, holocarpic, at maturity divided by transverse septa into a linear series of linklike sporangia or gametangia; zoosporangium with a single discharge tube; zoospores grape-seed-like, laterally biflagellate, incompletely cleaved within the sporangium and undergoing final maturation in an evanescent vesicle at the tip of the discharge tube; female gametangium

¹ Not considered in this text.

without periplasm, the contents after fusion with the male gamete forming a thick-walled resting spore, germination not observed; male gametangium like the female, conveying its contents to the female by a pore or tube formed in the cross wall.

Parasites of fresh-water algae and microscopic animals.

KEY TO THE SPECIES OF MYZOCYTIUM

Sporangia in regular beaklike chains, extramatrical part of the discharge tube narrowly cylindrical; in algae

Discharge tube narrowly cylindrical throughout . . . *M. proliferum*, p. 649

Discharge tube with a more or less well defined swelling beneath the inner face of the host wall *M. megastomum*, p. 652

Sporangia in somewhat irregular chains or forming an intricate complex, extramatrical part of the discharge tube broadly conical; in microscopic animals or their eggs

Sporangia in chains, broadly pyriform, oblong or more or less spherical; fertilization tube formed; in eel worms

M. vermicola, p. 653

Sporangia forming an intricate complex, irregularly saclike, often lobulate; fertilization pore formed; in rotifers

M. zoophthorum, p. 654

MYZOCYTIUM PROLIFERUM Schenk

Ueber das Vorkommen contractiler Zellen im Pflanzenreiche, p. 10.
Würzburg, 1858

(Figure 62 A-C, p. 651)

Pythium proliferum Schenk, Verhandl. Phys.-Med. Gesell. Würzburg, A. F., 9:27, pl. 1, figs. 30-41. 1859. Non de Bary, Jahrb. wiss. Bot., 2:182. 1860.

Pythium globosum Schenk, op. cit., 9:27, pl. 1, figs. 42-47. 1859.

Pythium globosum Walz, pro parte, Bot. Zeitung, 28:553, pl. 9, figs. 13-15. 1870.

Lagenidium globosum Lindstedt, Synopsis der Saprolegnieen, p. 54. Berlin, 1872.

Sporangia from one to twenty, in beadlike chains, broadly fusiform, broadly ellipsoidal and 15.7-26 μ long by 13-16 μ wide, or spherical and 14.4-25 μ in diameter, separated by two-layered refractive walls up to 2.4 μ thick, each forming a single narrowly cylindrical predominantly equatorial discharge tube about 2-3 μ in

diameter, which extends for a variable distance beyond the host wall; zoospores from four to twenty, bean-shaped, laterally biflagellate, 5.4–10 μ long by 3.6–6 μ wide, undergoing their final maturation in an evanescent vesicle formed at the orifice; female and male gametangia generally similar to the sporangia in size and shape or the female sometimes more spherical; oöspore spherical, 10–25 μ in diameter, lying loosely in the gametangium, with a smooth colorless double wall and a large eccentric globule, generally attached to the persistent fertilization tube, germination not observed.

Parasitic in *Spirogyra* sp., *Zygnema* sp., "Conferva," Schenk (*loc. cit.*), *Closterium didymotocum*, *C. acerosum*, *Cosmarium connatum*, Reinsch (1878:299, pl. 17, figs. 6, 9), *Zygnema* sp., *Spirogyra* sp., *Mougeotia* sp., *Mesocarpus* sp., *Cladophora* sp., *Oedogonium* sp., Zopf (1884:159, pl. 14, figs. 6–34), *Cladophora* sp., *Spirogyra* sp., *Zygnema* sp., Walz (*loc. cit.*), host (?), *Mesocarpus pleurocarpus*, Schroeter (1885:227), Minden (1915:430), *Closterium* sp., Cejp (1932a:5, pl. 1, figs. 11–13, pl. 2, fig. 5), GERMANY; various algae, Cornu (1869a:222), host (?), de Wildeman (1896b:46), FRANCE; *Spirogyra* sp. (coll. Marchal), de Wildeman (1893b:53, pl. 6, figs. 11–12), *Spirogyra* sp., *Zygnema* sp., de Wildeman (1895a:76, pl. 2, figs. 10–12), BELGIUM; host (?) (coll. Massart), de Wildeman (*loc. cit.*), NORWAY; *Mougeotia* sp., *Spirogyra* sp., Scherffel (1902b:109), *Mougeotia* sp., *S. mirabilis*, Domján (1936:51, pl. 1, figs. 95, 107, 125, 160–164), HUNGARY; *Mougeotia* sp., H. E. Petersen (1909:402; 1910:537, fig. 16e) DENMARK; *Closterium acerosum*, *Closterium* sp., *Cosmarium didymochondrum*, *Cosmarium* sp., *Spirogyra maxima*, *Spirogyra* sp., Voronichin (1920:11), RUSSIA; *Spirogyra* sp., Skvortzow (1927:206, fig. 10), CHINA; *Closterium angustatum*, W. G. Farlow (F. 586), *Cladophora* sp., Martin (1927:188, fig. 1 a–b), *Cladophora Kuetzingiana*, *Zygnema cruciatum*, Graff (1928:168), *Mougeotia* sp., (?) *Closterium acerosum*, Sparrow (1932b:288, fig. 4 a–c), *Mougeotia* sp., *Spirogyra* sp., Sparrow (1933c:532), *Spirogyra* sp., Thompson (1934:118, fig. 1 a–d), UNITED STATES; *Spirogyra* sp., Valkanov (1931a:365), BULGARIA; *Spirogyra affinis*, Chaudhuri (1931:472, figs. 1–7), INDIA; *Spirogyra Jürgensii*, *Spirogyra* sp., *Cladophora* sp., Tokunaga (1934a:228, fig. 2), JAPAN.

Constantineanu (1901:377, figs. 78–79) has reported this species from Rumania in *Cladophora* and *Spirogyra*. From his figures (all except 78b and 79a) of the sporangia and the one-globuled nature

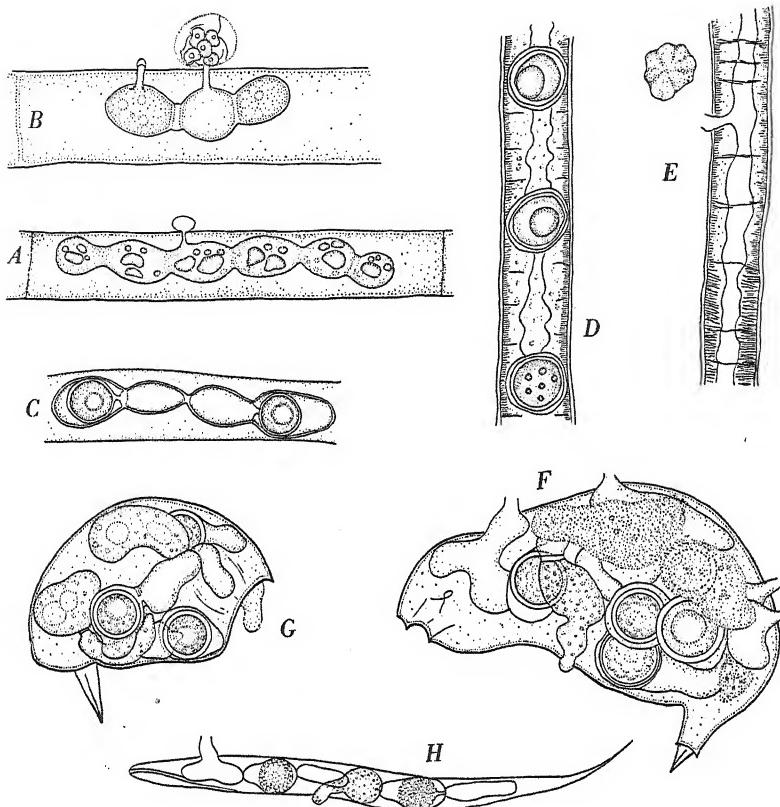


FIG. 62. Lagenidiaceae

A-C. Myzocytium proliferum Schenk in *Conjugatae*: *A*, one-celled thallus about to become segmented, cyst of zoospore and penetration tube still persistent; *B*, three-celled thallus ($\times 360$), one cell of which has become converted into a zoosporangium whose recently discharged zoospores are maturing at orifice of discharge tube; *C*, thallus ($\times 400$) in *Mougeotia* which has become converted into sex organs; the two outer cells are oögonia, each bearing an oöspore; the two inner cells are antheridia. *D-E. Resticularia nodosa* Dangeard in *Lyngbia*: *D*, endobiotic resting spores formed on thallus; *E*, protoplasm discharged and forming zoospores at orifice of discharge tube. *F-G. Myzocytium zoophthorum* Sparrow ($\times 400$) in rotifers, thalli bearing zoosporangia and sex organs. *H. Myzocytium vermicola* (Zopf) Fischer in eelworm, zoosporangia and sex organs in cadaver.

(*A-B*, Sparrow, 1932b; *C*, after Zopf, 1884; *D-E*, Dangeard, 1890-91b; *F-G*, Sparrow, 1936a; *H*, Zopf, 1884)

of the emerged zoospores, it is probable that he had a mixture of *Achlyogeton* and *Myzocytium*. The fungus figured by Martin (*loc. cit.*) differs from the usual form of this species in that the discharge tube is expanded just beneath the host wall. A form in *Closterium costatum* in the Farlow Herbarium (No. 642) shows a similar expansion. Whether or not this swelling is of significance in distinguishing these from *Myzocytium proliferum* is at present uncertain. The forms occurring in desmids (see *M. megastomum*, *M. irregulare*) always exhibit it. The fungus in *Closterium* reported by Sparrow (1932b) is doubtfully *M. proliferum*.

Although *Myzocytium proliferum* has been reported many times and, from the excellent illustrations of Zopf (1884), is well known, more data on the sizes of the parts are needed. The zoospores described by Tokunaga ($10 \times 6 \mu$), for example, are twice the size of those described by Sparrow ($5.4 \times 3.6 \mu$).

The sexual stage (Fig. 62 C) was first observed by Cornu (1869a).

As Zopf has pointed out, the species is most frequently found in shallow stagnant brightly lit water. It may occur in epidemic proportions from spring to fall, particularly on Conjugatae.

In some instances of zoospore discharge the vesicle may be so tenuous as to be nearly invisible. It has been described as entirely lacking in certain specimens (Thompson, *loc. cit.*). Chaudhuri (*loc. cit.*) states that in his material a fertilization tube was not formed by the male gametangium. Since his observations apparently refer to material fixed in formalin, it is possible that the tube had been present but soon dissolved in the preservative.

MYZOCYTIUM MEGASTOMUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 17:53, pl. 6, figs. 6-10, pl. 7, figs. 19-20.
1893

Sporangia ovoid, ellipsoidal, spherical, or sometimes pyriform or cylindrical, $9-26 \times 12-50 \mu$ (wide?), variable in number, occurring in beadlike linear series, separated by narrow cross walls, discharge tube frequently equatorial, narrowly or irregularly cylindrical, distinctly expanded just beneath the host wall, prolonged extramatrically for a variable distance, up to 150μ ; gametangia like the sporangia and often occurring with them; oospore spherical, $11-13 \mu$ in diameter, with a thick smooth double wall lying loosely in the gametangium, germination not observed.

In *Spirotaenia* *spi.*, *Closterium* *sp.*, *C. attenuatum*, de Wildeman (*loc. cit.*), BELGIUM; *Closterium* *sp.*, de Wildeman (1895a:77), SWITZERLAND; desmid (coll. Massart), de Wildeman (1896b:47, pl. 3, figs. 22-26), NORWAY; *Closterium acerosum*, Scherffel (1914:17), HUNGARY; *Closterium* *sp.*, Skvortzow (1925:431), MANCHURIA; *Closterium areolatum* (?), Berdan (1938:408, fig. 14), UNITED STATES.

Although the zoospores are as yet undescribed, it is probable that this species belongs in *Myzocytium*.

Certain inhabitants of *Euastrum* referred tentatively by de Wildeman (1895a:76, pl. 2, figs. 7-9) to *Myzocytium proliferum*, as well as others called *Olpidium immersum* by this same investigator (*ibid.*, p. 65, pl. 2, figs. 1-6), all from Switzerland, may be simplified forms of *M. megastomum*. The same might be said of the plant shown in Figure 16d of *M. irregulare* by Petersen (1909:402, fig. 16d; 1910:538).

MYZOCYTIUM VERMICOLA (Zopf) Fischer

Rabenhorst. Kryptogamen-Fl., 1 (4):75. 1892

(Figure 62 H, p. 651)

Myzocytium proliferum var. *vermicolum* Zopf, Nova Acta Acad. Leop.-Carol., 47:167, pl. 14, figs. 35-37. 1884.

Sporangia up to twelve in the host, somewhat broadly pyriform, oblong, or more or less spherical, the septa narrow, with one, occasionally two, short broadly conical discharge tubes protruding for a short distance beyond the host wall; zoospores discharged in a quickly evanescent vesicle at the tip of the discharge tube; oögonia pyriform or ellipsoidal; oöspore ellipsoidal or spherical, colorless, not filling the oögonium; antheridium smaller than the oögonium, narrow, somewhat oblong, with a delicate cylindrical penetration tube.

Parasitic in *Anguillula*, Zopf (*loc. cit.*), GERMANY; Dangeard (1903b:207, pls. 2-5), FRANCE; Valkanov (1931a:365), BULGARIA.

One-celled thalli were occasionally produced which became transformed into a single sporangium. Fischer (*loc. cit.*) believes *Bicricium lethale* Sorokin to be a two-celled form of this species. See, however, the remarks concerning *Bicricium* (p. 133).

Dangeard (*loc. cit.*) has described certain cytological details (see

p. 604) in this species and has observed the partial germination of the oöspores. The resting bodies, after several months, became multinucleate, vacuolate, and formed a germ tube. They probably then produced zoospores, although this was not observed. The species is considered rare, but Dangeard found that it occurred frequently in his laboratory cultures of eel worms.

MYZOCYTIUM ZOOPHTHORUM Sparrow

J. Linn. Soc. London (Bot.), 50:461, pl. 19, figs. 1-8, 10-14. 1936

(Figure 62 F-G, p. 651)

Sporangia variable in number, irregular, saclike, often lobulate, 5-17 μ in diameter, of variable length, separated by narrow inconspicuous septa, discharge tube generally short and broad; zoospores laterally biflagellate, 10-11 μ long by 6-7 μ wide, partly or wholly delimited within the sporangium, at discharge the first few zoospores forming an amorphous subspherical mass in a vesicle at the tip of the broadly conical evacuation tube, quickly becoming separated and undergoing their final maturation at the orifice, the vesicle almost at once disappearing; gametangia similar to the zoosporangia; oöspore spherical, colorless, 12-15 μ in diameter, with a thick smooth wall and a large eccentric globule, lying loosely in the gametangium, germination not observed; male gametangium conveying its contents into the female through a pore formed in the cross wall.

Parasitic on adults and eggs of rotifers, ENGLAND, DENMARK.

It is possible that the very tubular branched thallus shown by Sparrow (1936a: pl. 19, fig. 9) belongs to a species of *Lagenidium* rather than to *Myzocytium zoophthorum*. The strongly lobed thallus found in adult rotifers recalls *M. lineare* and, when these lobes are very pronounced, a species of *Lagenidium*, to which genus the fungus may possibly be referable. No specialized antheridial branch, outgrowth, or fertilization tube is ever formed, however, as is generally true of *Lagenidium*.

The zoospores are predaceous and attack moving adult rotifers, possibly attaching themselves by a mucilaginous secretion to the carapace of the host. The animal continues its activities until the thallus is well developed, when death ensues.

IMPERFECTLY KNOWN SPECIES OF MYZOCYTIUM

? *MYZOCYTIUM IRREGULARE* H. E. Petersen

Bot. Tidsskrift, 29:403, fig. XVI a, d. 1909; Ann. Mycologici, 8:538,
fig. XVI a, d. 1910

Sporangia short-cylindrical, globose, or irregular in shape, articulation variable, most frequently in pairs, often forming short branches when more than two, discharge tube of variable length, usually expanded beneath the host wall; zoospores and sex organs not observed.

In *Cosmarium sp.*, *Micrasterias sp.*, H. E. Petersen (*loc. cit.*), Sparrow, DENMARK; *Cosmarium sp.*, Scherffel (1914:17), HUNGARY; *Micrasterias rotata*, Cejp (1933a:8, pl. 1, fig. 16), (?) Type III on *M. denticula*, Reinsch (1878:300, pl. 17, figs. 8, 13), GERMANY; *Micrasterias sp.*, W. G. Farlow (F. 384), UNITED STATES.

As Petersen states, the inclusion of this fungus in *Myzocytium* rather than in *Lagenidium* is questionable. In the branched or lobed nature of its thallus it is closer to *Lagenidium*. A similar situation is found in *M. lineare* and *M. zoophthorum*. In the latter, however, the absence of a specialized antheridium appears to relate the species to *Myzocytium* rather than to *Lagenidium*. Since, apparently, no sex organs (or even zoospores) have as yet been described in the present fungus, the antheridial character cannot be used in this instance to determine the genus.

Schulz (1922:149, fig. 87) has figured in *Micrasterias rotata*, from Danzig, the empty sporangia and resting spores of a fungus which is very similar to *Myzocytium irregulare*.

The two-celled forms of this species resemble *Bicricium* (see p. 133).

? *MYZOCYTIUM LINEARE CORNU*

Ann. Sci. Nat. Bot., V, 15:21. 1872

Sporangia tubular, simple or branched, never ovoid, disposed in rows; oögonia very tubular, swollen, and irregular.

In desmids, FRANCE.

Cornu (1877b) has identified with his incompletely described species certain fungi found by Reinsch (1878:300, pl. 17, figs. 5, 14)

only in *Cosmarium spp.* (Type II). It is not clear from Reinsch's figure whether the twisted complex of tubes (*op. cit.*, fig. 5) consists of one or more cells. De Wildeman (1895a:57) doubts that the fungus belongs in *Myzocytium*. Cejp (1933a:8) also considers it disputable whether the form belongs to *Lagenidium* or *Myzocytium*, although he favors the latter. Since the zoospores were not observed by either Cornu or Reinsch the fungus may belong in the Chytridiales.

LAGENIDIUM SCHENK

Verhandl. Phys.-Med. Gesell. Würzburg, A. F., 9:27. 1859

(Figure 63, p. 660; Figure 64, p. 670)

Thallus endobiotic, monophagous or polyphagous, holocarpic, without specialized vegetative structures, either a one-celled and saccate body or a more or less extensive, irregularly branched or unbranched tube which at maturity becomes transversely segmented to form the rudiments of the zoosporangia or gametangia or both, contents at first having a dull clear lustrous matrix within which are imbedded more refractive, irregularly shaped large clods and fat droplets, later becoming evenly and coarsely granular and vacuolate, walls giving a cellulose reaction, cyst and infection tube frequently persistent; each of the zoosporangia bearing a single discharge tube, at least the tip of which is extramatrical; zoospores reniform, broadly fusiform or grape-seed-like, laterally biflagellate, fully formed in an evanescent vesicle at the orifice of the discharge tube, or cleaved out within the sporangium and completing their development in a more or less quickly evanescent vesicle, or, rarely (the primary spores?), moving within the sporangium and encysting at the orifice, movement after discharge generally an even swimming, rarely hopping; monoecious or dioecious, the gametangia shaped like the sporangia or the female often more rotund, monandrous, in rare instances lacking an antheridium, the male gametangium forming a fertilization tube, periplasm apparently lacking; oöspore borne singly and loosely (except in one species) in the female gametangium, with a thick wall, more or less coarsely granular parietal plasma, a large oil globule, and often a lateral bright spot, germination not (?) observed.

Parasitic in fresh-water algae, particularly in the vegetative filaments, gametangia, and zygotes of the Conjugatae, in pollen

grains; weakly parasitic in mosquito larvae, copepods and *Daphne*, and rotifer eggs. One species (*Lagenidium giganteum*) has been cultivated on artificial media.

One-celled thalli which are transformed at maturity into either zoosporangia or gametangia are occasionally formed by the multi-cellular species (for example, *Lagenidium Rabenhorstii*). Some species are, however, typically one-celled (Fig. 63, p. 660), and it is a question whether they should be retained in *Lagenidium* or segregated in a distinct genus. If segregation is considered feasible, the genus *Lagena* (Vanterpool and Ledingham, 1930; Truscott, 1933) exists for their accommodation.¹ In *Lagena*, thus far found only as an apparently obligate parasite in the roots of cereals and wild grasses, the one-celled or saccate or branched thallus, which is attached to the host wall at the point of infection, becomes transformed as a whole into a zoosporangium or a gametangium. The zoospores as well as the resting spore are formed as in dwarf one-celled individuals of *Lagenidium Rabenhorstii* or mature specimens of *L. Oedogonii*.

Although the primary zoospores are considered to be completely suppressed, as in *Pythium*, Scherffel has observed their encystment at the orifice, as in *Achlya*. In some instances of discharge the vesicle is apparently lacking and the spores are formed directly in the medium; in others the vesicle persists for only a short time; and in *Lagenidium Marchalianum* the spores are segmented before discharge and complete their maturation at the orifice, devoid, save for an instant, of any surrounding vesicle.

Certain species resemble in the complexity of thallus development and sexual reproduction an *Aphragmium* type of *Pythium*. Thus, in *Lagenidium giganteum* (Couch, 1935b) the branched threads may extend as much as 1-2 mm. from the host and the segments which will form the zoosporangia may be 50-300 μ long. Although in *L. Marchalianum* these sizes are not attained, here, too, the thallus is extensive and ramifies throughout the algal host in a strikingly *Pythium*-like manner (Fig. 64 B, p. 670). Further resemblance to *Pythium* is found in the sexual organs. These are more differentiated in *Lagenidium* than in *Myzocytium*, the antheridium in particular often appearing more specialized in form and generally

¹ Since no zoospores have been reported in *Lagenidiopsis*, a genus erected by de Wildeman to include a one-celled, dioecious fungus found only in the sexual stage, it cannot be considered here.

producing a fertilization tube rather than a simple pore. It is still not separated, however, from the antheridial branch by a cross wall as in the more highly developed species of *Pythium*. The assumption that the female gametangium lacks periplasm appears to rest entirely on morphological observations.

KEY TO THE SPECIES OF LAGENIDIUM

Thallus never septate, forming a single gametangium or zoosporangium

In fresh-water algae

In diatoms

Sporangium rounded or more or less flask-shaped, discharge tube short, blunt, thin-walled throughout *L. Cyclotellae*, p. 659

Sporangium tubular, unbranched, or occasionally with finger-like branches

Discharge tube very short, with a thick-walled "forcing apparatus"; resting spore lying loosely in the gametangium *L. brachystomum*, p. 661

Discharge tube prolonged somewhat extramatrically; resting spore filling the gametangium ... *L. enecans*, p. 662

In *Oedogonium* *L. Oedogonii*, p. 663

In rotifer eggs *L. oophilum*, p. 664

Thallus predominantly septate, at least when forming gametangia

Thallus typically forming a single sporangium, predominantly monoecious, the gametangia arising by septation of the thallus; in pollen grains *L. pygmaeum*, p. 664

Thallus typically forming more than one sporangium and gametangium, dioecious or monoecious; in green algae or animals

Thallus predominantly of small extent, monophagous

Thallus cylindrical or with irregular short straight or crooked branches; in vegetative cells of filamentous Conjugatae

Oöspore wall smooth *L. Rabenhorstii*, p. 665

Oöspore wall bullate *L. papillosum*, p. 667

Thallus regularly or irregularly tubular, forming a more or less intricate complex of irregularly branched segments

Segments more or less isodiametric, rarely torulose; in *Closterium* *L. intermedium*, p. 667

Segments more or less irregularly contorted; in gametangia and zygotes of filamentous Conjugatae

Segments thick, strongly contorted, with numerous short branches or lobulations; discharge tube 2μ in diameter, often swollen beneath the wall of the zygote; resting spore smooth or dentate

L. entophytum, p. 668

Segments slender, more regularly branched; discharge tube very delicate, expanded beneath the wall of the gametangium; resting spore always smooth

L. gracile, p. 669

Thallus extensive, mycelial, strongly polyphagous when parasitic in filamentous algae

In green algae

Discharge tube strongly expanded beneath the host wall;
in *Closterium* *L. Closterii*, p. 669

Discharge tube cylindrical throughout; in *Oedogonium*

L. Marchalianum, p. 671

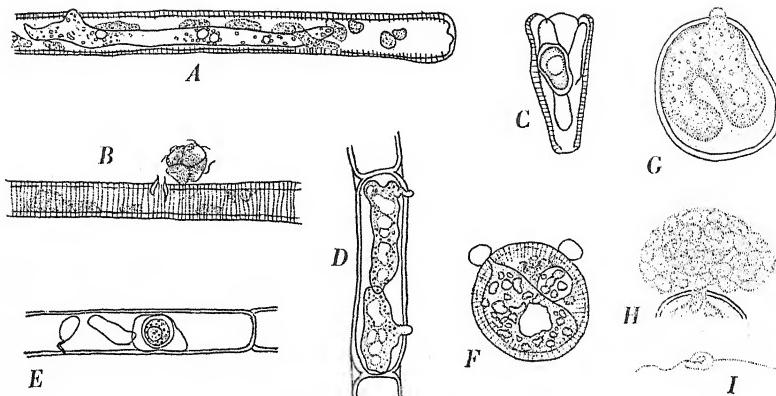
In microscopic animals and mosquito larvae.. *L. giganteum*, p. 672

LAGENIDIUM CYCLOTELLAE Scherffel

Arch. Protistenk., 52:18, pl. 2, figs. 49-59. 1925

(Figure 63 F, p. 660)

Thallus rounded, or by the formation of short lobes more or less irregularly saccate, one-celled, pushing apart the valves of the host, attached to the cyst of the infecting zoospore by the persistent infection tube, forming a single more or less flask-shaped sporangium with a short blunt discharge tube 3μ long by 3μ in diameter which protrudes between the separated valves of the host; zoospores from five to six, fully formed in the sporangium, within which motility is initiated, emerging individually from the discharge tube, (primary?) zoospores ovoid, about 6μ long by 3.5μ broad, with two oppositely directed flagella, about 6μ long, which arise subapically from the concave side of the body, contents bearing a posterior parietal refractive fat body, secondary zoospores not observed; sex organs dioecious, the gametangia like (?) the sporangia, wall of the male gametangium collapsing after fertilization; female gametangium completely filled by the resting spore; resting spore spherical, 10μ in diameter, or broadly ovoid or occasionally somewhat angular or irregular, $10-12 \mu$ long by $8-10 \mu$ wide, with a smooth thick colorless

FIG. 63. *Lagenidium*

A-C. *Lagenidium brachystomum* Scherffel ($\times 375$) in diatoms: A, vacuolate sporangium showing at the left the outgrowth which will become the discharge tube; place of attachment of infection tube was at extreme left tip of thallus; B, portion of frustule of *Synedra* from which protrudes the short discharge tube; zoospores are undergoing final maturation at orifice; C, mature oöspore in *Gomphonema*. D-E. *Lagenidium Oedogonii* Scherffel ($\times 250$): D, two vacuolate sporangia with discharge tubes; E, oöspore lying loosely within its container, the empty tubular contributing thallus attached to it; a small empty thallus with persistent infection tube is also shown. F. *Lagenidium Cyclotellae* Scherffel ($\times 500$) in *Cyclotella*, host with a large and a small thallus in it, empty epibiotic cysts of infecting zoospores persistent. G-I. *Lagenidium oophilum* Sparrow ($\times 500$) in rotifer eggs: G, nearly mature lobed sporangium with discharge tube protruding through wall of egg; H, tip of sporangium with zoospores almost completely discharged; flagella are beginning to form on emerged spores; I, single zoospore.

(A-F, Scherffel, 1925a; G-I, Sparrow, 1939c)

wall, dense glittering parietal contents, a large eccentric lustrous globule, and a lateral bright spot, germination not observed.

In *Cyclotella Kutziniana*, HUNGARY.

Scherffel justly emphasizes the close similarity of the zoospore discharge in this remarkable species to that in both *Olpidiopsis* and *Ectrogella*. The fungus also resembles most species of *Olpidiopsis* in that the resting spore completely fills the female gametangium. But he considers the persistence of the cyst and the infection tube

to be a fundamental character, marking the plant as a species of *Lagenidium*. Evidently no fertilization tube was formed by the male gametangium.

In the early stages of thallus development the content is typically lagenidiaceous, the hyaline smooth plasma bearing refractive irregularly shaped fat clods. Later, a large irregular vacuole always appears (Fig. 63 F). The zoospores are segregated in the parietal layer of cytoplasm lining a large central vacuole. Upon its disappearance the spore initials swell and fill the sporangium, though the cleavage lines remain sharply defined. No special forcing apparatus is formed, the valves merely being pushed apart by the expanding thallus. The zoospores resembled the primary type found in *Ectrogella Bacillariacearum*. Diplanetism, however, was not observed.

LAGENIDIUM BRACHYSTOMUM Scherffel

Arch. Protistenk., 52:21, pl. 2, figs. 70-85. 1925

(Figure 63 A-C)

Thallus tubular, very thin-walled, predominantly unbranched and 150-250 μ long by 4-7.5 μ in diameter, or with short or, rarely, somewhat elongate finger-like branches running parallel with the main axis, infection tube occasionally persistent, forming a single sporangium with a very short thick-walled cylindrical discharge tube which functions also as a forcing apparatus between the girdle bands of the host; zoospores few (from two to four) or numerous, grape-seed-like, laterally biflagellate, 6-8 μ long by 4 μ wide, formed in a vesicle at the orifice of the discharge tube; sex organs dioecious, gametangia resembling the sporangia; resting spore lying loosely in the female gametangium, spherical or broadly ovoid to oblong, 11-24 μ long by 6-10 μ broad, colorless, with a moderately thick smooth wall and with one or two large globules in the dense contents, germination not known.

Parasitic in *Synedra ulna*, *Cymbella cymbiformis* var. *parva*, *Gomphonema constrictum*, *Nitzschia linearis*, Scherffel (*loc. cit.*), HUNGARY; *Synedra* sp., Couch (1935b:385, figs. 20-21), UNITED STATES.

The species, according to Scherffel, differs from *Lagenidium enecans* in forming typically an unbranched sporangium (Fig. 63 A) and a very short discharge tube which is not prolonged extramatrically (Fig. 63 B). Further, the valves are not split apart, but forced.

Mixed infections of this species, *Ectrogella Bacillariacearum*, and *E. monostoma* may occur in *Synedra ulna*. When this happens the type of zoospore discharge, the character of the contents, and the method of exit of the discharge tube are used in differentiating the members of the complex.

The fungus found by Couch apparently lacks the thick-walled forcing apparatus.

LAGENIDIUM ENECANS Zopf

Nova Acta Acad. Leop.-Carol., 47:154. 1884

Thallus completely tubular, 6-12 μ in diameter by 37-156 μ long, or with a few short broad finger-like branches, sometimes somewhat contorted and saccate, the infection tube persistent, transformed into a single sporangium, the discharge tube cylindrical, 3-6 μ in diameter by 9-36 μ long, prolonged only slightly extramatrically, forming a thick-walled forcing apparatus between the girdle plates; zoospores grape-seed-like, biflagellate, 8-12.5 μ long by 5.7 μ broad, produced in a vesicle at the orifice of the discharge tube, movement rapid, irregular; sex organs dioecious, gametangia resembling (?) the sporangia; resting spore probably formed after fusion of the contents of a female gametangium with those of an adjacent irregularly spherical male gametangium, filling (?) the receptive gametangium, spherical, 18 μ in diameter, broadly ovoid or irregular and with strongly indented contour, 15-22 \times 20-24 μ , with a smooth thick wall, a large central lustrous fat globule, and from one to several bright spots in the finely granular contents, germination not observed.

In *Stauroneis Phoenicentron*, *Cocconema lanceolatum*, *Pinnularia spp.*, Zopf (*loc. cit.*), GERMANY; (?) diatom, de Wildeman (1893a:9; 1893b:44, pl. 4, fig. 32), BELGIUM; *Cymbella gastrooides*, *Pinnularia viridis*, *Amphora ovalis*, *Cymatopleura solea*, *Stauroneis Phoenicentron*, Scherffel (1902a:[106]; 1925a:20, pl. 2, figs. 60-69); *Navicula cuspidata*, *N. cuspidata* var. *ambigua*, *Stauroneis Phoenicentron*, Skvortzow (1925:483), MANCHURIA.

The species was only briefly described by Zopf, without figures. Most of our knowledge of it rests on the investigations of Scherffel. Cook (1935:78) states that the sexual organs were observed by de Wildeman (*loc. cit.*), but the latter merely mentions having found

an organism possibly referable to this species and gives one figure of an empty sporangium.

LAGENIDIUM OEDOGONII Scherffel

Hedwigia, 41:(105). 1902; Arch. Protistenk., 52:109, pl. 5, figs. 209-219. 1925
(Figure 63 D-E, p. 660)

Thallus irregularly saccate or ovoid, sometimes with broad finger-like prominent lobes or short branches, occasionally tubular and simple or coiled, variable in size, $20-25 \times 35-52 \mu$, infection tube and zoospore case often persistent, forming a single sporangium with one, generally short, discharge tube, which is slightly constricted when passing through the host wall (rarely two discharge tubes); zoospores grape-seed-like, 6μ long, furrowed, with a prominent bright spot (vacuole?), predominantly formed in a vesicle at the orifice of the discharge tube, capable of repeated emergence, rarely assuming motility within the sporangium, emerging individually and encysting at the orifice, cysts 4μ in diameter, escaping as secondary laterally biflagellate zoospores; sex organs dioecious, the female gametangium resembling the sporangium; resting spore spherical, $12-14 \mu$ in diameter, lying loosely in the gametangium, with a smooth colorless wall 2μ thick, contents with a parietal layer of coarse granules and a large eccentric lustrous fat globule, germination not observed; male gametangium smaller, often somewhat tubular.

Parasitic in *Oedogonium* sp., Scherffel (*loc. cit.*), Domján (1936:52, pl. 1, figs. 170, 180-181), HUNGARY; *Oedogonium* sp., Couch (1935b: 386, figs. 22-31), *Oedogonium* sp., Sparrow (ITHACA, NEW YORK), UNITED STATES.

The *Achlya*-like behavior of the zoospores in rare instances might perhaps be interpreted as repeated emergence or dicystism in the sense of Coker and Matthews (1937:15), not as diplanetism. Emergence of the spores in *Pythium*-like fashion, followed by repeated emergence has been noted by Couch (1935b: figs. 32-34) in what may be a small form of this species.

Scherffel points out that in sexual reproduction there is definite distinction between the male and the female gametangia, the former being smaller and often more tubular than the latter (Fig. 63 E). This is of particular interest since it appears to indicate that here degree of thallus development is not correlated with degree of differen-

tiation of the sexual organs. However, further observations are needed on this phase of the species.

Careful studies of the development of this species have been made by both Scherffel and Couch. Each of these investigators noted the production of a small appressorium by the infecting zoospore and the formation of a protective layer of callus by the host. The parasite reduces the chloroplasts to a brownish residue, the cytoplasm and starch being almost completely consumed.

LAGENIDIUM OOPHILUM Sparrow

Mycologia, 31:532, figs. 1-15. 1939

(Figure 63 G-I, p. 660)

Thallus when occurring singly somewhat irregularly saccate or ellipsoidal, with broad lobes of varying length, when several, more regularly ellipsoidal and often unlobed, converted holocarpically into a single thin-walled colorless sporangium 20-40 μ long by 12-25 μ wide with a short sessile or slightly prolonged discharge papilla 4-5 μ in diameter; zoospores grape-seed-like, laterally biflagellate, 8 μ long by 6 μ wide, discharged individually and undergoing a period of maturation in a group at the orifice of the discharge tube, apparently not surrounded by a vesicle; cystospore 5-6 μ in diameter; sexual reproduction not observed.

Parasitic in eggs and embryos of rotifers, UNITED STATES.

LAGENIDIUM PYGMAEUM Zopf

Abhandl. Naturforsch. Gesell. Halle, 17:96, pl. 1, figs. 29-31, pl. 2, figs. 1-12. 1887

Thallus tubular, contorted, with irregular lobulations, or spherical, ovoid, ellipsoid, or reniform, frequently single, occasionally from two to four in the host cell, forming a single sporangium provided with a broad short somewhat irregular occasionally basally branched discharge tube; zoospores broadly fusiform, 16-18 μ long, laterally biflagellate, segmented in the sporangium, completing their development in a vesicle at the orifice; sex organs monoecious, rarely dioecious, gametangia resembling the sporangia but somewhat stouter, formed by the septation of a single thallus, occasionally a second septum delimiting a sporangium, female gametangium strongly expanded, sometimes with papilla-like outgrowths; resting

spore spherical, lying loosely in the gametangium, 18–29 μ in diameter, with a smooth double wall, contents with a large globule, germination not observed; male gametangium irregular, forming a fertilization tube.

Parasitic in pollen grains of *Pinus sylvestris*, *P. austriaca*, *P. Laricio*, *P. Pallasiana*, Zopf (*loc. cit.*), GERMANY; coniferous pollen grains, Maurizio (1895), de Wildeman (1895a:74), SWITZERLAND; pollen grains of different plants, H. E. Petersen (1909:401; 1910:537), DENMARK; (?) pollen, Voronichin (1920:12), RUSSIA; pollen of *Pinus strobus*, Sparrow, UNITED STATES (MASSACHUSETTS).

Schulz (1923:181, figs. 4–7) has reported this species from Danzig in *Cosmarium pyramidatum* and pine pollen. With the exception of the organism in his Figure 7 (in pine pollen), those shown are hardly identifiable with *Lagenidium pygmaeum*.

From the fact that the sex organs are predominantly monoecious and are formed by septation of a single thallus, it is probable that the species is capable of multicellular development under less restricted environmental conditions and that it is not comparable with truly one-celled, dioecious forms.

Zopf observed that, because of the great numbers of zoospores, widespread infection of new pollen could be induced under laboratory conditions in twenty-three hours.

LAGENIDIUM RABENHORSTII Zopf

Sitzungsber. Bot. Vereins Prov. Brandenburg, 20:77. 1878; Nova Acta Acad. Leop.-Carol., 47:145, pl. 12, figs. 1–28, pl. 13, figs. 1–9. 1884

(Figure 64 D, p. 670)

Thallus of small extent, monophagous, cylindrical or with frequent irregularities and with short or long often clavate, straight, crooked, or irregular branches 2.5–8 μ in diameter, occasionally somewhat irregularly saccate; sporangia from one to ten, generally from five to seven, delimited by narrow sometimes slightly constricted septations, variable in shape, with a cylindrical or slightly conical discharge tube which is rarely locally constricted when passing through the host wall and which projects only slightly extramatrically; zoospores reniform, 8.5 μ long by 6 μ wide, laterally biflagellate, formed in a vesicle at the orifice of the discharge tube; sex organs dioecious or, less frequently, monoecious, the female gametangium intercalary, lateral

or terminal, expanded, spherical, ovoid, fusiform, or irregular, 15–16 μ wide; oospore spherical, with a smooth colorless double wall, lying loosely in the gametangium, 10.4–20 μ in diameter, with a fairly large nearly centric globule, germination not (?) observed; male gametangium resembling the sporangium or occasionally somewhat crook-necked, laterally applied, with a fertilization tube.

Parasitic in vegetative cells of *Spirogyra* sp., *Mesocarpus* sp., *Mougeotia* sp., etc., Zopf (*loc. cit.*), Schroeter (1885:227), Minden (1915:434), GERMANY; (?) *Spirogyra* sp., de Wildeman (1895b:98, figs. 1–2), FRANCE; *Spirogyra* sp., Constantineanu (1901:379), RUMANIA; *Spirogyra* sp., Scherffel (1914:17), *Spirogyra* sp., *Zygnema* sp., Domján (1936:51, pl. 1, figs. 56, 94, 174), HUNGARY; *Spirogyra* sp., Atkinson (1909a:329, fig. 5 A–B), *S. orthospira*, *Oedogonium plusiosporum*, Graff (1928:169), *Spirogyra* sp., Sparrow (1932b:289, fig. 4d), *Mougeotia* sp., Sparrow (MICHIGAN), UNITED STATES; *Spirogyra* sp., Cook (1932a:142, figs. 39–45; 1935:75, pl. 1, figs. 1–14, pl. 4, figs. 1–8), GREAT BRITAIN.

This species, well known from the excellent researches of Zopf, has, with one exception (Graff, *loc. cit.*), been reported only in Conjugatae. In early spring it occurs usually in the sporangial stage. By midsummer, according to Zopf, the thalli are mostly converted into gametangia.

Both Atkinson and Cook have noted the lack of a vesicle during zoospore formation, and it is probable that under certain conditions this structure deliquesces soon after the emergence of the protoplasm. The antheridium, particularly on monoecious individuals, may be strikingly differentiated from the ordinary segment of the thallus and may assume, as Zopf (1884: pl. 12, fig. 26) and Sparrow (1932b: fig. 4d) have shown, a shape reminiscent of the crooknecked type found in *Pythium*.

One-celled thalli, transformed either into sporangia or gametangia, have been described by Zopf, but are atypical.

Germination of the oospore in this species (the only occurrence known in the genus) has been reported by Cook (1935) to be as follows: Soon (twenty-four hours) after formation of the resting-spore wall it breaks down and a single nearly spherical biflagellate zoospore 8 μ in diameter is liberated, which after a short period of activity comes to rest on a healthy host cell and infects it. This spore gains

access to the outside medium by the "breaking down" of the algal wall, presumed by Cook to be achieved by natural agencies such as wind and water currents. Although the quick germination of resting structures is recorded in other fungi, the "breaking down" of the wall and, in particular, the highly inefficient process of liberating only a single zoospore from a sexually formed structure are rare, if not unknown, among these plants and need confirmation.

LAGENIDIUM PAPILLOSUM Cocconi

R. Accad. Sci. Istituto Bologna, Mem. Ser. V, 4:362, figs. 1-3. 1894

Thallus resembling that of *Lagenidium Rabenhorstii*; sex organs monoecious, oögonia and antheridia like those of *L. Rabenhorstii*; oöspore lying very loosely and centrically in the oögonium, with a thick smooth inner wall and a densely bullate outer wall.

In *Spirogyra sp.*, Cocconi (*loc. cit.*), ITALY; *Spirogyra sp.*, Voronichin (1920:12), RUSSIA.

The mature oöspore was observed in some specimens to be surrounded by residual protoplasm, termed "periplasm" by Cocconi.

The sporangial stage, from the figures, is somewhat anomalous. Zoospores are pyriform and biflagellate, the flagella appearing apically attached.

LAGENIDIUM INTERMEDIUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 19:97, pl. 4, figs. 10-13. 1895

Thallus tubular, complex, more or less isodiametric, rarely torulose, with short or long irregular branches; sporangia relatively few, each composed of a cylindrical element or of a complex of branches, discharge tube very narrowly cylindrical, sometimes slightly expanded beneath the host wall and locally constricted when passing through the wall, frequently prolonged extramatrically; zoospores not observed; (?) resting spore intercalary, spherical, with a thick smooth wall, germination not observed; antheridium not observed.

In *Closterium Ehrenbergii*, FRANCE.

A resting structure was observed in only one instance and was tentatively considered to be the resting spore.

The thallus resembles superficially *Lagenidium entophytum*, but in its regularly cylindrical elements approaches *L. Rabenhorstii*. In

spite of the lack of observations on the zoospores, the fungus is probably correctly referred to *Lagenidium*.

LAGENIDIUM ENTOPHYTUM (Pringsheim) Zopf

Nova Acta Acad. Leop.-Carol., 47:154, pl. 13, figs. 10-18, pl. 14, figs. 1-5.
1884

(Figure 64 A, p. 670)

Pythium entophytum Pringsheim, Jahrb. wiss. Bot., 1:289, pl. 21, fig. 1.
1858.

Myzocytium entophytum (Pringsheim) Cornu, Ann. Sci. Nat. Bot., V,
15: 21. 1872.

Lagenidium americanum Atkinson, Bot. Gaz., 48:336, fig. 6. 1909.

Thallus consisting of an irregularly contorted bent relatively thick tube bearing numerous short lateral variously oriented lobulations or short branches; sporangia few, consisting of irregularly tubular lobulate segments of varying length, delimited by thick refractive septate constrictions, the single discharge tube of each segment cylindrical or somewhat irregular, 2μ in diameter, of variable length, often swollen at the point of contact with the inner wall of the host and locally constricted where it passes through the wall; zoospores reniform, laterally biflagellate, $5-7 \mu$ long by $4-6 \mu$ wide, formed at the orifice of the discharge tube, possibly surrounded by a vesicle; oöspore lying singly and loosely in a tubular segment of the thallus, spherical, with a thick golden smooth or slightly dentate outer wall, parthenogenetically formed, germination not observed.

Parasitic in the zygote of *Spirogyra* sp., Pringsheim (*loc. cit.*), zygote and zygospores of *Spirogyra* sp., Zopf (*loc. cit.*), Minden (1915:436), (?) *Euastrum humerosum*, *Micrasterias Mahabaleshwrensis* var. *Wallichii*, Schulz (1923:181), GERMANY; *Spirogyra* sp., de Wildeman (1895b:100, pl. 3, figs. 24-25), (coll. Lemaire) de Wildeman (1896b:47), FRANCE; host (?), Scherffel (1904:117), HUNGARY; *Spirogyra varians*, *S. insignis*, *S. calospora*, Atkinson (*loc. cit.*), UNITED STATES; *Spirogyra maxima*, Voronichin (1920:12), RUSSIA.

Lagenidium americanum Atk. is said to differ in the lack of a swelling on the discharge tube, but the figures do not seem to bear out this statement. From Zopf's description and figures this swelling is apparently not a constant feature.

The fungus described by Cook (1935:77, pl. 2, figs. 15-25, pl. 3,

figs. 33-35) from Great Britain, though occasionally branched, does not possess the distinctly tubular, contorted, and lobulate appearance characteristic of Zopf's fungus. The sporangia are 12-15 μ long by 4-6 μ in diameter, the zoospores 8 μ long by 4 μ in diameter, and the parthenogenetically developed oospores spherical and 12 μ in diameter. Further study may show this to be a new species.

Fischer (1892:82) states that Carter (1856) had confused this fungus with the developmental stage of an *Astasia*-like flagellate.

LAGENIDIUM GRACILE Zopf

Nova Acta Acad. Leop.-Carol., 47:158. 1884

Thallus tubular, somewhat irregular, coiled, branched, slender, 4.5 μ in diameter, forming a series of cylindrical or spherical sporangia, each provided with a very narrowly cylindrical discharge tube which is expanded beneath the wall of the host gametangium (but not the zygospore) and extends for a short distance extramatrically; zoospores bean-shaped, 7.5 μ long by 4 μ wide, with two equal flagella, formed in a vesicle at the tip of the discharge tube; female gametangium intercalary, rarely terminal, spherical or nearly so; resting spore parthenogenetically formed, lying loosely in the gametangium, spherical, 13-14 μ in diameter, with a thick smooth wall, germination not observed.

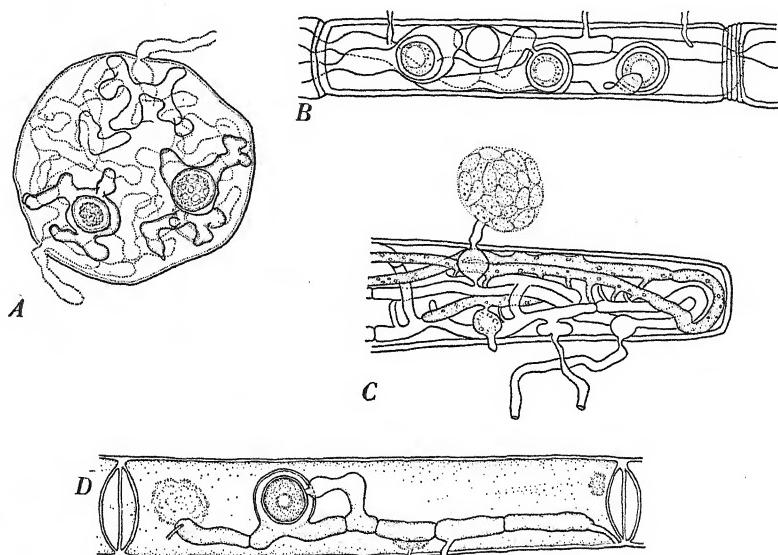
In the gametangia of *Spirogyra* sp., Zopf (*loc. cit.*), GERMANY; gametangia and zygospores of *Spirogyra* sp., *S. Grevilleana* (coll. Lemaire), de Wildeman (1895b:102, fig. 3), FRANCE; zygospores of *Spirogyra* sp., Cook (1932a:140, figs. 32-38; 1935:77, pl. 3, figs. 26-32), ENGLAND.

Differing from *Lagenidium entophytum* in its more slender, more regularly branched thallus, very slender discharge tube, and smooth-walled resting spore. Zopf has stated that the thallus may extend from one host cell to another. It is possible that this statement refers to the discharge tube.

LAGENIDIUM CLOSTERII de Wildeman

Ann. Soc. Belge Micro. (Mém.), 17:43, pl. 6, figs. 1-5. 1893
(Figure 64 C, p. 670)

Thallus extensive, branched, more or less isodiametric or somewhat expanded and irregular, straight or twisted, about 1.8-2.8 μ

FIG. 64. *Lagenidium*

A. *Lagenidium entophytum* (Pringsheim) Zopf ($\times 270$) in zygospore of *Spirogyra*, zygospore cleared to show contorted thallus; extramatrical discharge tubes and two resting spores may be seen. B. *Lagenidium Marchalianum* de Wildeman ($\times 460$) in *Oedogonium*, portion of filament showing sex organs, and empty cylindrical zoosporangia each with discharge tube. C. *Lagenidium Closterii* de Wildeman ($\times 420$) in *Closterium*, portion of host cell showing cylindrical empty sporangia and one sporangium forming its zoospores in a vesicle at orifice of discharge tube. D. *Lagenidium Rabenhorstii* Zopf ($\times 540$) in *Spirogyra*, empty sporangia and monoecious sex organs.

(A, D, Zopf, 1884; B-C, Couch, 1935b)

in diameter; sporangia of variable length, delimited by narrow septa, discharge tube produced as a lateral outgrowth, which forms a large spherical or subspherical structure just beneath the host wall, constricted locally when passing through the wall, more or less prolonged extramatrically, up to $20-30 \mu$, cylindrical; zoospores bean-shaped, laterally biflagellate, $5.6-6.3 \mu$ long by 3.8μ wide, formed in a vesicle at the orifice of the discharge tube, movement hopping or describing a smooth spiral path; sex organs dioecious, female gametangium much expanded; resting spore spherical, not filling the oögonium,

10–12 μ in diameter, with a thick double wall, the outer surface irregularly papillate, contents with a large globule, germination not observed; male gametangium cylindrical, with a prolongation which makes contact with the female gametangium.

In *Cladophora rostratum* (and *C. striolatum*?), de Wildeman (*loc. cit.*), BELGIUM; parasitic in *Cladophora sp.*, Cejp (1933a:7, pl. 1, figs. 17–18, pl. 2, fig. 4), GERMANY; *Cladophora sp.*, Couch (1935b:381, figs. 35–38), UNITED STATES; *Cladophora sp.*, H. E. Petersen (1909: 402; 1910:537), DENMARK.

As Couch has pointed out, before the sporangia are delimited the well-developed mycelial thallus of this species strongly resembles that of an *Aphragmium* type of *Pythium*. Whether a fertilization tube is formed, as seems probable, is not clear from de Wildeman's description.

LAGENIDIUM MARCHALIANUM de Wildeman

Ann. Soc. Belge Micro. (Mém.), 21:10, pl. 1, figs. 1–9. 1897

(Figure 64 B)

Thallus predominantly narrowly cylindrical, 2.2–9 μ in diameter, with occasional irregularly expanded parts up to 13 μ in diameter, especially near the point of infection, sparingly branched, ramifying through many cells of the host, strongly constricted and only 1 μ in diameter when passing through the cross walls, cyst and infection tube persistent; sporangia delimited by narrow cross walls, generally unaccompanied by constrictions, 30–90 μ long by 5–9 μ in diameter, each with a single lateral cylindrical discharge tube 1.5–3 μ in diameter and up to 30 μ long extending for varying distances extramatrically; zoospores few (often only four), grape-seed-like, with a shallow furrow, a vacuole, and a few refractive globules in the clear plasma, delimited within the sporangium and completing their maturation at the orifice of the discharge tube, the vesicle quickly disappearing at discharge; sex organs monoecious or dioecious, female gametangium monandrous, rarely parthenogenetic, intercalary, rarely terminal, formed from an expanded segment, up to 20 μ in diameter; resting spore lying loosely in the gametangium, spherical, 8–18 μ in diameter, contents with a large eccentric globule, wall smooth, thick (3 μ), germination not observed; male gametangium a somewhat expanded segment either adjacent to the female gametangium

or arising as a short lateral subtending branch of the adjacent cell or as a short lateral branch of another thallus, forming a fertilization tube.

Parasitic in vegetative cells of *Oedogonium sp.*, de Wildeman (*loc. cit.*), BELGIUM; *Oedogonium sp.*, Couch (1935b:384, figs. 39-40), Sparrow (MICHIGAN), UNITED STATES.

This species, like *Lagenidium Closterii* and *L. giganteum*, closely resembles an *Aphragmium* type of *Pythium*, not only in its predominantly cylindrical hypha-like thallus, but in its strongly polyphagous habit and sex organs. The antheridium, however, still remains an undifferentiated segment of the thallus, and this, together with the lagenidiaceous aspect of the cytoplasm, marks the fungus as belonging to *Lagenidium*.

It appears to be a true parasite; efforts to propagate it on dead cells were unsuccessful.

Occasionally the filament of the parasite as it emerges from the cross wall is covered for a short distance with a rough layer of wall material laid down by the living host in a futile effort to stop further invasion. A similar formation has been noted by Scherffel and Couch on the infection tube of *Lagenidium Oedogonii*.

LAGENIDIUM GIGANTEUM Couch

Mycologia, 27:376, figs. 1-19. 1935

"The main hyphae are segmented, being constricted or not constricted at the septum, the segments sometimes separating from each other; branched. When growing on a copepod, *Daphne*, or mosquito larva, the large segmented hyphae are within the host, but numerous delicate hyphae extend from the host for a distance of one or two millimeters to form a fringe which has much the appearance of a delicate species of *Aphanomyces*. Hyphae 6-40 μ thick, the segments 50-300 μ long. The hyphal walls contain cellulose giving a purplish reaction with chlor-iodide of zinc. The protoplasm has the pale whitish gleam as in the *Ancylistales*. Any segment may become a sporangium. The sporangium empties its content in an undifferentiated, naked mass (or sometimes several masses) through a tube, the dimensions of which are 6-10 \times 50-300 μ . This mass becomes differentiated into a variable number of laterally biciliate zoospores.

Zoöspores $8-9 \times 9-10 \mu$, their movement as in *Achlya* but rather sluggish. Monoplanetic. Sexual reproduction not observed.

"Weakly parasitic on mosquito larvae, copepods and *Daphne*. Also culturable as a saprophyte" (Couch, *loc. cit.*).

The species is of exceptional interest, as Couch has indicated, in the hypha-like nature of the thallus—resembling strongly in this an *Aphragmium* type of *Pythium*—and in being readily cultured on a variety of artificial media. Couch suggests that, from the character of the thallus development, it is intermediate between the filamentous and nonfilamentous Phycomycetes. Observations on the sexual organs, thus far not reported, will probably determine to which group it is more nearly related. A highly organized sexual apparatus—for example, an oögonium containing periplasm and a well-defined antheridium—might indicate that the species is closer to *Pythium*, perhaps to *P. Daphnidarum*, than to *Lagenidium*.

Infection experiments on living mosquito larvae were inconclusive in demonstrating the parasitic ability of the species.

In the course of cultural studies a mycelial sector appeared which was composed of irregularly branched hyphae mostly 12μ in diameter and which formed an open rameose rather than a compact type of growth. Further transfers indicated the stability of this mutant.

IMPERFECTLY KNOWN SPECIES OF LAGENIDIUM

? LAGENIDIUM ELLIPTICUM de Wildeman¹

Ann. Soc. Belge Micro. (Mém.), 17:8, pl. 1, figs. 1-11. 1893

Thallus consisting of a single irregularly swollen contorted lobulate tube with filamentous prolongations; zoospores not observed; resting spores ellipsoidal, $20-30 \mu$ long by $10-14 \mu$ wide, with a thick wall provided with irregularly placed blunt protuberances, contents refractive and granular, without a large globule.

In rhizoids of mosses, BELGIUM.

In de Wildeman's Figure 2 what appear to be two short cylindrical discharge tubes are shown. A thorough investigation of the fungi occurring in this peculiar habitat will probably result in the refinding of this well-marked species. Obviously, further data on the reproductive organs are necessary to place the fungus generically.

¹ Not strictly aquatic.

? LAGENIDIUM SACCULOIDES Serbinow

Défense des Plantes, 2(2):84. 1925

(Description in Russian. No figures.)

A figure of this species may be found in Jaczewski (1931:67). The antheridial cell is narrowly ellipsoidal, and the oöspores (?) are spherical or ellipsoidal, with a papillate outer wall.

? LAGENIDIUM SYNCYTIORUM Klebahn

Jahrb. wiss. Bot., 24:265, pl. 3, figs. 22-24. 1892

Thallus a straight or irregularly curved filament 3-5 μ in diameter, becoming expanded in beadlike fashion and producing more or less irregular lateral outgrowths, which, by bending under, may form several layers and fill the host cell; sporangia numerous, of different shapes, spherical and 8-10 μ in diameter or oblong, curved or with blunt outgrowths, less often in beadlike chains, separated by narrow cross walls, discharge tube lateral, short, slightly prolonged extramatrically; zoospores and gametangia unknown.

Parasitic in sexual filaments of *Oedogonium Boscii*, GERMANY.

Known only from preserved material. Attacked *Oedogonium* cells were at first little affected by the parasite; nuclear division was not hindered. Cross walls were not, however, laid down by the alga. Up to four cells of normal size and nearly normal shape, lacking cross walls, could be found in which the fungus had been living.

De Wildeman (1895c:218) has tentatively identified a sterile *Lagenidium* in single cells of *Oedogonium* with this species. He suggests that *Aphanistis pellucida* Sorokin may be referable to this fungus.

? LAGENIDIUM ZOPFII de Wildeman

Bull. Soc. Belge Micro., 16:139. 1889-90

Thallus tubular, with irregular cylindrical or inflated branches, extending through several cells of the host; zoospores not observed; parthenogenetic (?) female gametangia expanded; resting spore spherical, about 14 μ in diameter, with a roughened wall.

In *Oedogonium*, BELGIUM.

? LAGENIDIUM SP. Deckenbach

Flora, 92:253. 1903

(The fungus is merely mentioned by Deckenbach, no description being given.)

In *Chaetomorpha aerea*, RUSSIA (BALACLAVA, BLACK SEA).

The binomial *Lagenidium Chaetomorphae* Jacz. has been given the plant by Jaczewski (1931:67).

? LAGENIDIUM SP. Scherffel

Arch. Protistenk., 52:23, pl. 2, fig. 86. 1925

Thallus tubular, somewhat irregular, with short lateral saccate outgrowths, infection tube persistent; sporangia several, delimited by narrow cross walls, discharge tube cylindrical, forming a thick-walled hourglass-like forcing apparatus which pushes apart the valves of the host, not extended appreciably extramatrically; zoospores not observed, possibly formed as in *Pythium*; sex organs dioecious (?), female gametangium irregularly expanded; resting spore spherical, not filling the gametangium; male gametangium like the sporangium, with a lateral outgrowth.

In *Pinnularia* sp., HUNGARY.

IMPERFECTLY KNOWN GENERA OF THE LAGENIDIALES

? LAGENIDIOPSIS DE WILDEMAN

Ann. Soc. Belge Micro. (Mém.), 20:115. 1896

Thallus endobiotic, tubular, with occasional short branches, holocarpic, without a specialized vegetative system, forming the rudiment of a single male or female gametangium, cyst and infection tube of zoospore persistent; zoosporangia and zoospores not observed; sex organs dioecious (?), the female gametangium swollen locally and, after fertilization, bearing in it the thick-walled resting spore, germination not observed; male gametangium smaller than the female, broadly expanded distally where it is applied to the female gametangium, separated from the concomitant thallus by a cross wall, forming a fertilization tube.

In oögonia of Characeae.

The genus, though strongly resembling *Lagena*, must remain of uncertain systematic position until the zoospores are described. The persistence of the cyst and infection tube lend weight to its being correctly placed in the Lagenidiaceae. De Wildeman is not certain whether the organism is always dioecious. In some specimens the male gametangium appeared to be formed by septation of the thallus into two gametangia.

? *LAGENIDIOPSIS REDUCTA* de Wildeman

Ann. Soc. Belge Micro. (Mém.), 20:115, pls. 6-7. 1896

Characters of the genus. Resting spore spherical or ellipsoidal, 13-19 μ in diameter, lying loosely in the gametangium, with a thick rough wall, contents granular, with one or several large globules, after fertilization the gametangium collapsing somewhat and soon disintegrating.

In oögonia of Characeae, SWITZERLAND.

? *RESTICULARIA DANGEARD*

Le Botaniste, 2:96. 1890-91. Emend. F. E. Fritsch, Ann. Bot. London, 17:661. 1903

(Figure 62 D-E, p. 651)

"Mycelium in part endophytic, in part ectophytic. Endophytic mycelium moniliform with or without transverse septa, occasionally forming chlamydospores; ectophytic mycelium with or without septa, generally strongly branched and forming thin- or thick-walled spores. Other portions of the ectophytic mycelium act as infecting-hyphae. Sporangia formed in the endophytic mycelium, the contents of which are protruded to the outside through the wall of the host and there split up into a small number of zoospores, the latter rather large and uniciliate" (Fritsch, *loc. cit.*).

On blue-green algae.

Only two investigators, Dangeard and Fritsch, have thus far made any significant observations on members of this problematical genus. Although both studied what is presumed to be the same species (*Resticularia nodosa*), certain important differences are noted in their accounts. Dangeard describes the resting structure as a zygospore sexually formed, whereas Fritsch terms it a chlamydospore produced

by simple expansion and the subsequent surrounding of an intercalary or apical segment of the filament with a thick wall. A second difference is found in the nonsexual reproduction. In *Pythium*-like fashion Dangeard's fungus formed at the tip of a short cylindrical tube several large posteriorly uniflagellate zoospores, which exhibited a typical chytridiaceous type of movement. No zoospore formation was observed by Fritsch either in *R. nodosa* or in his new species, *R. Boodlei*, even though the latter was kept under observation for several months.

If we accept the emended account of *Resticularia* as given above, or include Dangeard's description of zygosporre formation, the genus as a member of the Lagenidiaceae is anomalous, although not without a parallel among the chytrids. In *Coenomyces consuens*, also parasitic on blue-green algae, a similar type of irregularly septate thallus is developed and posteriorly uniflagellate zoospores are formed. The latter, however, are not matured outside the sporangium as they are in *Resticularia*. In *Zygochytrium* the thallus is tubular and non-septate, but the zoospores are extruded in a vesicle as a homogeneous mass and undergo their maturation outside the sporangium.

It is entirely possible that Fritsch and Dangeard were dealing with two distinct organisms living in blue-green algae, although the similarity of the figures given makes this improbable. It is also possible that the fungus which produced zoospores in Dangeard's algae was different from that forming the resting structures. This has some support from the fact that resting spores and sporangia are not figured on the same thallus. At all events, a detailed study of the development and reproduction of *Resticularia* will be necessary before the genus can be accepted without reservation and before its relationships to the other Phycomycetes can be understood.

? RESTICULARIA NODOSA Dangeard

Le Botaniste, 2:96, pl. 4, figs. 24-31. 1890-91. Emend. F. E. Fritsch,
Ann. Bot. London, 17:661, pl. 29, figs. 19-29. 1903

(Figure 62 D-E, p. 651)

"Endophytic mycelium (diam. 4-6 μ) usually septate, and forming numerous chlamydospores (diam. 6-9 μ), ectophytic mycelium very fine (diam. .5-1 μ), much branched, forming numerous chlamydospores, singly on lateral branches. Infecting-hyphae rare. Endo-

phytic mycelium commonly branched. Zoospores occasionally formed . . ." (Fritsch, *loc. cit.*).

In filaments of *Lyngbya Aestuarii*, Dangeard (*loc. cit.*), FRANCE; *Tolypothrix* sp., Fritsch (*loc. cit.*), ENGLAND.

The resting spores of Fritsch's fungus were dark brown and without a large central globule. Dangeard's were colorless and contained a large central globule. A sterile form recorded by Sparrow (1932b: 289, fig. 4g) in *Tolypothrix* may or may not belong here. Both this and the following species strongly resemble Fungi Imperfecti.

? RESTICULARIA BOODLEI F. E. Fritsch

Ann. Bot. London, 17:661, pl. 29, figs. 1-18. 1903

"Endophytic mycelium (diam. 5-8 μ) with occasional septa; ectophytic mycelium relatively broad (diam. 1.5-5 μ), much branched, forming numerous large thin-walled spores (diam. 12-15 μ), generally in a chain on lateral branches. Infecting hyphae abundant. Endophytic mycelium rarely branched. Zoospores not observed" (Fritsch, *loc. cit.*).

In filaments of *Tolypothrix* sp., ENGLAND.

? RESTICULARIA OEDOGONII Skvortzow

Arch. Protistenk., 51:432, fig. 14. 1924

Endobiotic thallus branched, 1-1.7 μ in diameter, several in a host cell, extramatrical thallus very delicate; resting spores from one to two in a host cell, 11.5-18.5 μ long by 7.4-11.1 μ broad, with a thick smooth colorless wall and a large oil globule nearly filling the lumen.

In filaments of *Oedogonium*, MANCHURIA (northern part).

PERONOSPORALES (PYTHIACEAE)

THE Peronosporales are a large order of primarily terrestrial microscopic fungi parasitic for the most part on flowering plants. One family, the Pythiaceae, is transitional so far as habitat is concerned, some of its members being distinctly aquatic, others amphibious, and still other terrestrial. Though certain monographers, notably Schroepter (1893), have placed the Pythiaceae in the Saprolegniales, it is considered by most students to be undoubtedly a member of the Peronosporales (Fischer, 1892). The following brief discussion is concerned primarily with the Pythiaceae, since it contains the only aquatic species of the order.

The genera of the Pythiaceae which have aquatic species are *Pythium*, *Pythiogeton*, *Zoopagrus*, and *Pythiomorpha*. Strong reasons have been advanced in recent years for considering *Pythiomorpha* an aquatic saprophytic *Phytophthora* with internally proliferous sporangia (see particularly Buismann, 1927; Drechsler, 1932), and when its morphology is better known, particularly that of the sexual stage, it may be found advisable to merge it with the older genus.¹ Since Miss Matthews (1931) has brought together the material on aquatic as well as terrestrial species of *Pythium*, the reader is referred to her monograph and to the older one of Butler (1907) for details of the aquatic species of this genus.² These are found as parasites and saprophytes of algae, microscopic animals, and bits of debris of plant and animal origin. Although the genus has been regarded as confined to fresh water, soils, and phanerogams, one species has been described in recent years on decaying marine Rhodophyceae (Sparrow, 1934c). *Pythiogeton* is, morphologically, closely related to *Pythium*; it occurs mostly on twigs and fruits, often in very foul water.

¹ Blackwell, Waterhouse, and Thompson (*Trans. Brit. Mycol. Soc.*, 25: 148-165. 1941) have summarized convincingly the arguments against maintaining *Pythiomorpha* distinct from *Phytophthora*.

² Many other species of *Pythium*, some of them aquatic, have been reported since the publication of Miss Matthew's book. See in particular *P. apleroticum* Tokunaga (*Trans. Sapporo Nat. Hist. Soc.*, 14:12. 1935), in *Spirogyra*; *P. akanese* Tokunaga (*op. cit.*, 12:122. 1932), in *Aegagrophila* and *Cladophora*; *P. marinum* Sparrow (1934c). See also *Diosporangium Jonesianum* Höhnk (1936).

Pythiomorpha occupies similar substrata, but usually under conditions offering a better oxygen supply. *Zoophagus* is frequently found ramifying between algal filaments and between plants of *Chara* and *Nitella*. It is of unusual interest because of its predaceous habit of capturing and parasitizing actively moving microscopic animals. Nearly all species of the Pythiaceae have been cultivated successfully on artificial media.

DEVELOPMENT AND MORPHOLOGY

THE THALLUS

The vegetative body of the Pythiaceae is a well-developed, usually much-branched, slender mycelium, which in actively growing parts is nonseptate except where reproductive organs are delimited. With age, however, occasional septations may separate empty from viable parts of the hyphae. Demonstration of a cellulose reaction in the walls of the hyphae is difficult to achieve (Butler, 1907). In aquatic species the mycelium runs from cell to cell, whereas in the terrestrial, parasitic ones, such as those belonging to *Phytophthora*, it is also intercellular, haustoria being formed which absorb materials from the host cells. Gemmae are produced in certain species of *Pythium* (Butler, 1907:20), in *Zoophagus* (Arnaudow, 1921, 1925; Karling, 1936c), and in *Pythiomorpha* (Ito and Nagai, 1931; Höhnk, 1936). Ward (1883), Butler (*op. cit.*), and later investigators have found irregular toruloid swellings or budlike processes on the mycelium of *Pythium* under certain environmental conditions. Some (see Drechsler, 1925) have considered these to be intimately connected with nonsexual reproduction, but this is not true in all instances (Sparrow, 1931a). Irregularities of the mycelium and twisted complexes of the hyphae are also exhibited by species of *Pythiomorpha* (Petersen, 1910; Kanouse, 1925; Ito and Nagai, *op. cit.*).

In certain aquatic species of *Pythium* parasitic on algae (Sparrow, 1931a, 1931b) clusters of clavate or sickle-shaped appressoria are formed wherever the tips of the hyphae come into contact with the substratum. These become cemented to the algal wall by concave hyaline adhesion discs; from the face of each of these anchoring organs a tube develops which penetrates the algal wall. Inside, a hypha of typical diameter is produced. Similar appressoria may be formed within the alga. Appressoria are also found in at least one species of *Pythiogeton* (Drechsler, 1932). Another specialized mycelial struc-

ture may be mentioned. It occurs in species of *Zoophagus* and is a lateral outgrowth adapted to capturing rotifers. In *Z. insidians* (Sommerstorff, 1911; Mirande, 1920; Arnaudow, 1921, 1925; Gicklhorn, 1922; Sparrow, 1929) the extensive hyphae bear numerous short upright peglike branches, the tips of which secrete a mucilaginous material. The rotifer, coming into contact with these tips becomes stuck, and its body eventually is penetrated by a hyphal outgrowth. In *Z. tentaculum* (Karling, 1936c) the lateral branch bears a more specialized capturing device, which consists of from one to five narrow tentacles formed at the apex. No mucilaginous secretion could be demonstrated in this species.

Well-defined thick-walled chlamydospores have been reported in *Pythium* (Dissmann, 1927; Matthews, 1931).

REPRODUCTION

Nonsexual Reproduction

In the aquatic species of the Pythiaceae zoosporangia and zoospores are produced. The sporangia are of three main types: (a) an undifferentiated portion of the mycelium set off by cross walls and bearing an evacuation tube, (b) a complex of irregular digitate or lobulate intercommunicating elements set off by cross walls from the rest of the hyphae and having an evacuation tube, and (c) a bursiform, utriform, spherical, or somewhat ovoid terminal or intercalary structure set off by septa from the more or less differentiated hyphae, with or without a discharge tube. Intergrades between some of these types apparently occur and make difficult identification of an organism on this basis alone. Somewhat specialized sporangiophores are formed in *Pythiomorpha* and in the terrestrial genus *Phytophthora*.

Formation of zoospores.—In the aquatic Pythiaceae, with the exception of *Pythiomorpha*, the zoospores are formed outside the sporangium, from an amorphous mass of protoplasm. In *Pythium* and possibly also in *Zoophagus* this process takes place in a delicate somewhat spherical vesicle produced at the tip of the discharge tube. In *Pythiogeton*, however (Mindén, 1916; Drechsler, 1932), the vesicle is elongate and quickly disappears, leaving the protoplasmic mass, previously concentrated in its distal part, to undergo cleavage into zoospores free in the water. Under humid conditions and occasion-

ally when submerged (Minden, *op. cit.*; Drechsler, *op. cit.*) the protoplasmic mass may, in *Pythiogeton*, be shot out with explosive force. Sometimes this ejaculation occurs at the beginning of the evacuation of the sporangium, at other times, after the contents have completely emerged into the vesicle.

Zoophagus and many of the aquatic species of *Pythium* exhibit an undifferentiated sporangium resembling that in certain species of *Lagenidium*. The sequence of changes as they occurred prior to and during the formation of zoospores in *P. adhaerens* (Sparrow, 1931b) parasitic on the green alga *Rhizoclonium* is as follows: Numerous vacuoles appear in the densely granular contents of the mycelium, but after several hours decrease in size and at last disappear. In the finely granular protoplasm narrow cross walls laid down at considerable intervals along the mycelium may be observed. These blocked-off hyphal portions are the initials of the zoosporangia. The tips of certain hyphae (one for each continuous mycelial segment) now show striking modifications, which indicate that the contents will be evacuated through them. Within the apical curvature of these hyphal tips a narrow zone of hyaline very refractive material develops, which, seen in optical section, looks like a slender crescent (Fig. 65 A). This substance is apparently derived from the apical wall. At the same time, and often before the refractive dome becomes visible, there may be detected, in surface view, a vacuole immediately below the hyphal tip; this vacuole increases in size and perceptibility with the enlargement of the apical material. When viewed in optical section the glistening dome appears to have, shortly before the discharge of the contents, a double contour (Fig. 65 B-C). With the expansion of the apical refractive material protoplasmic ejection is initiated. The dilatation of the refractive dome keeps pace with the effluent protoplasm, and forms around it an extremely tenuous vesicle. This structure is never exactly spherical because the somewhat flaring tip of the evacuation tube protrudes slightly into its lower portion (Fig. 65 D). The ejected protoplasm appears as a smoothly granular homogeneous mass which completely fills the vesicle. Immediately after discharge a slight surging movement of the minute particles of the protoplasm is discernible, and after a few seconds slight contractions in certain regions lend a lumpy irregular appearance to the mass (Fig. 65 E). Faint peripheral lines of cleavage, which demarcate irregularly polygonal areas, soon become visible in the now slightly more contracted contents. About three

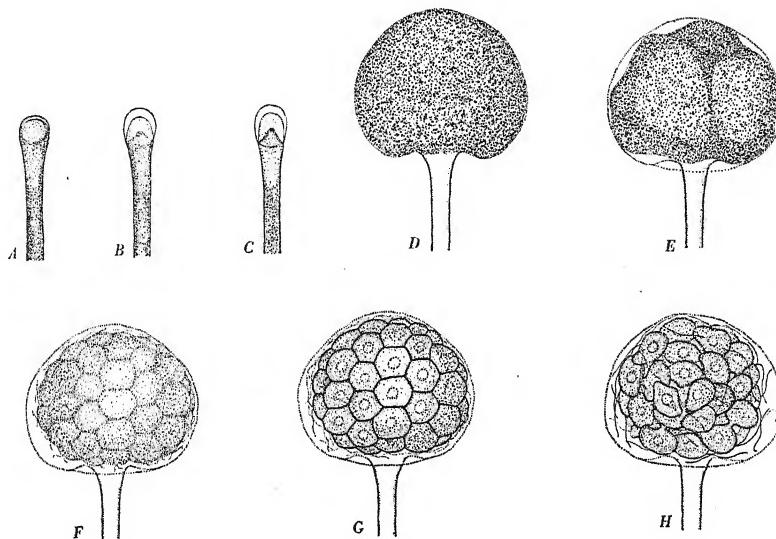


FIG. 65. Formation of zoospores in *Pythium*
(See explanation in text, p. 682. [Sparrow, 1931b])

minutes after discharge a rocking movement of the mass is noticeable. The lines of cleavage have by this time definitely delimited the spore initials (Fig. 65 F), which exhibit a slight individual movement approximately six minutes after the discharge. Short hyaline flagella may now be definitely seen around the periphery. The movement of the spore initials gradually becomes more pronounced, assuming a twisting or writhing character as the spore masses slowly become separated from one another. At about eight minutes after discharge a small vacuole becomes visible in each; the previously short hyaline flagella have increased in length by this time and appear as flexible lashes (Fig. 65 G). Three minutes later the spores have become nearly mature individuals. They still continue, however, to oscillate somewhat until they are perfectly formed (Fig. 65 H). About fourteen minutes after egress this motion is gradually superseded by a frenzied milling around of the zoospores within the confines of the vesicle. Finally the vesicle is ruptured, usually in the upper portion, by one or more zoospores, and the mature swarmers escape. The vesicle is ultimately dissolved into the surrounding medium.

In the lobulate and sphaerosporangial species of *Pythium* the

sequence of zoospore formation in the vesicle is essentially like that just described.

There is considerable disagreement among observers of *Pythiomorpha gonapodyides* (Petersen, 1910; Minden, 1916; Kanouse, 1925; Cejp, 1933b) as to its method of zoospore discharge. The sporangium is a somewhat ovoid structure with a blunt, rounded apex. According to Petersen, Kanouse, and Cejp, the zoospores are produced in the sporangium and, under favorable conditions, emerge as mature motile bodies not surrounded by a vesicle. Minden, on the other hand, states that, although the zoospores are formed within the sporangium, those which first emerge are surrounded for a short time by a vesicle derived from the material of the apical papilla. Occasionally emergence without a vesicle was observed. It is evident, then, if these investigators are all dealing with the same species of organism, that here, as in certain of the closely related Lagenidiaceae, variations occur with respect to the length of time during which the vesicle persists.¹ In *Pythiomorpha*, as in *Pythiogeton*, *Phytophthora megasperma* (Drechsler, 1931), and certain of the sphaerosporangial species of *Pythium*, formation of new sporangia occurs by internal proliferation (Fig. 69 B, G-H, p. 704).

The zoospore of all members of the Pythiaceae is of the laterally biflagellate, "secondary," type. It is usually capable of repeated emergence.

Sexual Reproduction

Sexual reproduction in the Pythiaceae is oögamous, usually only a single egg being produced in each oögonium. The oögonia and antheridia may be formed on the same hypha (monoclinous or androgynous) or on different ones (diclinous). If the antheridium arises directly beneath or near the oögonium on the same hypha it is said to be hypogynous. According to Arnaudow (1925), *Zoopaghus* is dioecious (heterothallic).

The development and structure of the sex organs are best known in *Pythium*. In the aquatic *P. adhaerens* and *P. angustatum*, for example (Sparrow, 1931b), the oögonia originate as terminal or intercalary swellings of the hyphae, which gradually increase in

¹ In *Pythiomorpha Miyabeana* (Ito and Nagai, 1931) the zoospores swim away directly upon emergence, whereas in *P. Oryzae* they are surrounded for a short time by a vesicle.

size until they are, when finally mature, spherical bodies cut off by cross walls from the adjacent hyphae. The antheridia in these species are diclinous in origin, although occasionally androgynous, and arise as short lateral expanded hyphal branches, which clasp the oögonium early in its formation. From two to five antheridia are generally in contact with an oögonium, the single hypha from which they usually arise often surrounding the female gametangium in *P. adhaerens* (Fig. 66 A, p. 686). When fully mature each antheridium is delimited from the hypha by a cross wall, formed generally at about 15 μ from its tip, which is in contact with the oögonial wall (Fig. 66 B). Fertilization is accomplished in from three to five hours by the gradual transference of all, or nearly all, of the antheridial contents to the oögonium through a cylindrical refractive tube, about 2 μ in diameter, which penetrates the wall of the oögonium and extends an unknown distance into the oöplasm (Fig. 66 C).

Coincidently with the formation of the fertilization tube, the contents of the oögonium become more condensed and contract away from the wall (Fig. 66 C, p. 686). The oöplasm, connected by hyaline strands of protoplasm to the oögonial wall, generally lies in an eccentric position, in close contact with the part of the wall penetrated by the fertilization tube. During fertilization the contents, instead of having a smooth densely granular consistency, become darker and extremely irregular in contour. As the discharge of antheridial material progresses, the oöplasm continues to contract and the fine droplets of oil which are distributed throughout it combine to form large, irregularly shaped, highly refractive bodies, which finally compose nearly the whole mass.

After fertilization the contour of the oöspore grows more even, the refractive bodies rapidly decrease in size, and the protoplasm becomes coarsely granular. No periplasm could be observed in living material.¹ There is now formed around the oöplasm a thin pellicle which gradually thickens. Finally, during the formation of the wall, the oil droplets dispersed throughout the somewhat mottled oögonial protoplasm fuse into a large centrally disposed refractive globule, whose diameter is usually about one third that of the oöspore (Fig. 66 D-E, p. 686). Between the inner face of the wall and the

¹ According to Patterson (1927), periplasm in *Pythium torulosum* was difficult to demonstrate even by cytological methods. On the other hand, it was relatively conspicuous in living material of *P. dictyosporum* (Sparrow, 1931a).

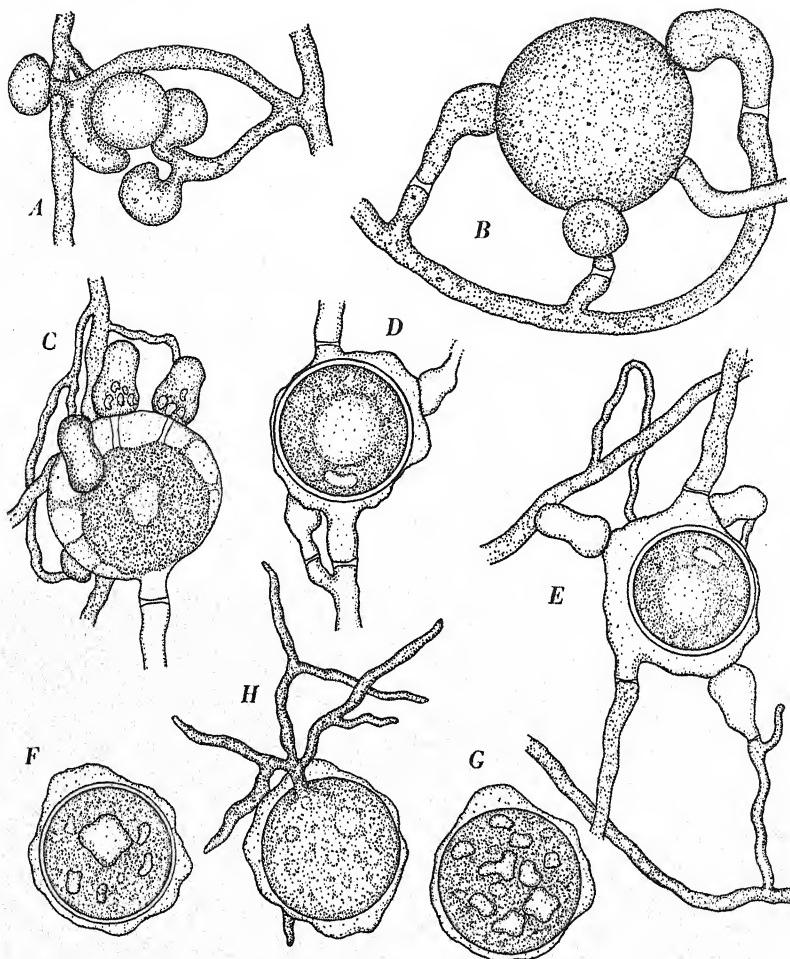


FIG. 66. Sexual reproduction in *Pythium*

A-B. Two stages in development of oögonia and antheridia of *Pythium adhaerens* Sparrow: *A*, antheridial rudiments encircling central oögonial rudiment; *B*, antheridia delimited from their hyphae by cross walls. *C-H.* Sex organs of *Pythium angustatum* Sparrow and germination of oöspore: *C*, terminal oögonium to which is attached a cluster of diclinous antheridia with their fertilization tubes piercing the contracted oöplasm; *D*, mature oöspore with one androgynous (lower) and one diclinous antheridium persistent on oögonium; *E*, oöspore to whose oögonium three diclinous antheridia are

oil globule a lenticular structure, probably a nucleus, appears. The mature oöspore in this species lies loosely within the oögonial wall. After a rest period it germinates. In this process the large oil globule disassociates into a number of refractive parts (Fig. 66 F) that become regularly dispersed throughout the now evenly and finely granular protoplasm. Coincidently with these changes, the oöspore wall steadily decreases in thickness, apparently being absorbed by the protoplasm (Fig. 66 G). The germ hypha, somewhat constricted as it pierces the spore wall, elongates, branches, and establishes the new mycelium (Fig. 66 H). In water certain of its branches may be converted into sporangia. Only vegetative development takes place in nutrient solutions.

In *Pythiogeton* sex organs are probably formed, but absolute proof of their occurrence is as yet lacking. This deficiency is largely due to the failure of the sex organs to develop in pure culture and to the inability of the observer to trace with certainty in gross culture the connection between the sexual and the nonsexual phases. Minden (1916) found two somewhat similar types of sex organs in his material, one of which he associated with *P. utriforme*, the other with *P. transversum*. The former type had been previously observed by Thaxter (1895b) in association with *Gonapodya*, a genus that is frequently found growing in the same habitat as *Pythiogeton*. It has since been recorded by at least two other investigators (Lund, 1934; Sparrow, 1936a). In both instances, as in Minden's cultures, it was found in conjunction with sporangia of *P. utriforme*. The other type, associated with *P. transversum*, has evidently not been reported since Minden's time.

In what are presumably the sex organs of *Pythiogeton utriforme* the rudiments of the antheridia and the oögonia arise, according to Minden (1916), as two small vesicles of about equal size, in contact with one another and, at least in some plants, on the same hypha. One of these swellings, the antheridium, which frequently is sub-terminal on its supporting hypha, fails to grow larger, whereas the other, the oögonial rudiment, expands and becomes packed with

attached; F, oöspore starting to germinate; large globule is broken up and wall is beginning to be resorbed; G, oöspore with wall nearly completely resorbed; H, branched hyphal system produced by germinating oöspore.
(All $\times 1100$.)

(Sparrow, 1931b)

spherical or angular refractive structures. During development of the oögonium the supporting hypha is drained of its contents. The mature antheridium is hemispherical, with its broad face in contact with the oögonial wall. It forms a blunt fertilization tube which pierces the oögonium and which probably conveys into it the antheridial contents. Minden evidently did not observe the actual process of fertilization. No periplasmic material is discernible, and no contraction of the oögonial contents occurs. After fertilization the droplets in the oögonium gradually disappear, and coincidently a bright refractive "halo" becomes visible on the periphery of the contents. This marks the initiation of formation of the oöspore wall. The hyaline material continues to replace the granular contents until finally at maturity only a small spherical central part composed of cytoplasm remains. The mature oöspore consists, then, of a small sphere of living contents, within which a conspicuous reserve globule may frequently be found, and an extremely thick hyaline, shining, concentrically layered wall, the outer surface of which is in close contact, if not actually fused, with the wall of the oögonium. The ripe oöspores are usually formed within or near the surface of the substratum and it is this fact together with the fragility of the slender mycelium on which they are borne which makes it difficult in gross culture to connect them with absolute certainty to the extramatrical mycelium bearing the zoosporangia.

The sex organs associated by Minden (1916) with *Pythiogeton transversum* were similar in their general configuration to those of *P. utriforme*, but differed in certain respects. The first divergence is in the helical involvement of the supporting hyphae of the sex organs. Whereas there can be seen in Minden's Plate 6, Figure 62, of *P. utriforme* a slight tendency for the oögonial stalk to twist around that of the antheridium, his description and figures of the sex organs of *P. transversum* indicate that the oögonial hypha may make as many as four or five turns around the supporting element of the male organ. Occasionally the reverse situation was found. A second, even more striking, difference is to be discerned in the external configuration of the mature oögonia of the two species. This is spherical in *P. utriforme* but in *P. transversum* it was distinctly polygonal, and the spherical oöspore with its strikingly thickened wall lay free within the oögonium.

Stages in the germination of the oöspore of what is supposedly

Pythiogeton utriforme have recently been observed (Sparrow, 1936a). The first indication of germination was a slight increase in the amount of the protoplasmic contents and the appearance of faint shadowy areas of indefinite shape in the thick hyaline wall. After twelve hours the large reserve globule in the contents disappeared, the central granular cytoplasm increased in size, and around the periphery of this cytoplasm a large number of short spinelike protuberances appeared. During the succeeding twenty-four hours the contents expanded further, at the expense of the refractive wall, and at the same time became densely granular. The spines increased in breadth and their tips touched the inner wall of the oögonium. In another twenty-four hours the contents almost reached the oögonial wall and the spines again became only short peripheral attenuations. Subsequently the spines completely disappeared and the contents occupied the whole oögonium. A discharge tube was then produced, through which, presumably, the contents were ejected. Although the true nature of these curious spines was not determined, it is possible that they are vacuoles. (See Fig. 68 J-N, p. 698.)

The sex organs of *Pythiomorpha gonapodyides* are not unlike those of *Pythium*. They were not observed by Petersen (1910), but Minden (1916) subsequently described immature ones. Other descriptions of the sexual apparatus of what is presumably this species have been given by Kanouse (1925), Cejp (1933b), and Forbes (1935a). The structures figured by Miss Kanouse differ from Minden's, notably in the shape of the antheridium and its relation to the oögonium. In her material the supporting hypha wound around the oögonium and the antheridium was applied broadly to the oögonium rather than only at its tip. Similar sex organs are figured by Cejp. The mature oöspore has a thickened wall, completely fills the oögonium, and, from the figures of Miss Kanouse and Cejp, does not possess a large reserve globule. At germination one or more hyphae are produced (Kanouse, *op. cit.*); zoospores, however, are never formed. Miss Forbes's material differed from that of Miss Kanouse in two particulars. First, the oöspore, while filling the oögonium, contained a large reserve globule. Secondly, the basally applied antheridium was clavate and its supporting hypha showed no involvement whatsoever with the hypha of the oögonium. In *Pythiomorpha Fischeriana* the oöspore is apogamously developed (Höhnk, 1936). Ito and Nagai (1931) describe typically pythiaceous

sex organs for *Pythiomorpha Miyabeana*. In this species involvement of the antheridial by the oögonial stalk is sometimes evident. The oöspore exhibits a large oil globule and lies loosely in the oögonium. From this summary of the various types of sexual organs which have been described for *Pythiomorpha* it is evident, as Drechsler (1932) stated, ". . . that representatives of at least two groups of Pythiaceous fungi, separated by very obvious differences in their more distinctive antheridial relationships and in oöspore structure, have been assigned to *Pythiomorpha*."

SYSTEMATIC ACCOUNT

PERONOSPORALES

THE aquatic members of the Peronosporales are the aquatic species of the Pythiaceae. The characters are those given below for that family.

PYTHIACEAE

Microscopic, aquatic, amphibious, or terrestrial saprophytic or parasitic fungi; thallus a richly branched hyphal complex, cross walls in vigorously growing parts formed only to delimit reproductive organs; thick-walled chlamydospores and gemmae sometimes formed; zoosporangia either undifferentiated portions of the mycelium, or an irregularly expanded complex of lobulate elements and an evacuation tube, or an ovoid, spherical, or bursiform structure with or without a more or less prolonged evacuation tube, formed singly or in catenulate series, sometimes internally proliferous; zoospores of the reniform laterally biflagellate type, either formed outside the sporangium in a vesicle or free in the water or produced within the sporangium, capable of repeated emergence; oögonia terminal or intercalary, spherical or cylindrical, smooth or spiny-walled, usually containing a single egg, which is often differentiated into oöplasm and periplasm; antheridia terminal or intercalary, rarely lacking, diclinous or androgynous, hypogynous, or amphigynous, each forming a well-defined fertilization tube; oöspore lying loosely in the oögonium or

completely filling it, smooth or rough-walled, upon germination producing a germ tube or zoösporangium.

Parasites of algae, flowering plants, and microscopic animals; saprophytic on both plant and animal substrata.

KEY TO THE AQUATIC GENERA OF THE PYTHIACEAE

Zoosporangium an undifferentiated portion of the mycelium

 Hyphae bearing short lateral branches adapted to the capturing
 of rotifers *ZOOPHAGUS*, p. 691

 Hyphae not bearing such branches *PYTHIUM*¹

Zoosporangium differentiated from the mycelium, consisting either
 of a complex of lobulate elements and an evacuation tube or of
 a somewhat bursiform, spherical, or ovoid enlargement with or
 without an evacuation tube

Zoospores formed within a vesicle produced at the tip of an
 evacuation tube; oöspores with a moderately thick wall. *PYTHIUM*¹

Zoospores either extruded as an undifferentiated mass in an
 elongate quickly evanescent vesicle or differentiated within
 the sporangium; oöspore wall very thick or not unusually so

Zoospores extruded as an undifferentiated mass in an extremely
 long quickly evanescent vesicle; oöspore wall extremely
 thick *PYTHIOGETON*, p. 695

Zoospores differentiated within the sporangium, usually
 emerging as separate motile swarmers; oöspore wall not
 unusually thick *PYTHIOMORPHA*, p. 702

ZOOPHAGUS SOMMERSTORFF

Oesterr. botan. Zeitschr., 61:372. 1911

(Figure 67, p. 694)

Mycelium delicate, extensive, the main hyphae sparingly branched, the hyphae bearing numerous short peglike lateral branches modified for the capturing of moving rotifers, septate or nonseptate gemmae sometimes formed; zoosporangium consisting of an undifferentiated portion of the mycelium; zoospores formed in a vesicle produced at the tip of the discharge tube, of the laterally biflagellate

¹ The aquatic species of this genus are not treated in the account which follows, since Miss Matthews (1931) has already presented them in detail. For aquatic species reported since the publication of her monograph see page 679, note 2.

type, capable of repeated emergence; sex organs dioecious, antheridium clavate, single, oögonium bearing a single egg.

Parasitic on rotifers.

Zoosporangia and sex organs have been recorded thus far only in *Zoophagus insidians*, and there somewhat imperfectly. Sommerstorff (*loc. cit.*) states with respect to nonsexual reproduction that in one instance he found near the open end of a hyphal branch protruding from a rotifer rounded cysts and a group of about eight bodies of amoeboid shape which were simultaneously twisting and oscillating. The moving bodies soon came to rest and encysted. When next observed they had apparently emerged from their cysts through a short germ tube. Arnaudow (1921) describes the zoosporangium as similar to the completely filamentous type found in certain species of *Pythium* and asserts that the zoospores are formed as in this genus. Zoospore formation was not observed by Karling in *Z. tentaculum* (see the discussion under *Z. insidians*). Sexual organs have been described apparently only by Arnaudow (1925).

Valkanov (1932) considers that the carnivorous aquatic fungi *Synchaetophagus* (Apstein, 1910), *Hydatinophagus*, *Sommerstorffia* (Arnaudow, 1923a, 1923b), and *Zoophagus* are all closely related and should be placed in a special group of the Saprolegniaceae. The reasons he gives are not convincing. From the morphological evidence now at hand, although this is admittedly scanty, it seems more likely that the curious carnivorous habit has been evolved by members of several groups of aquatic Phycomycetes.

KEY TO THE SPECIES OF ZOOPHAGUS

- Capturing organ consisting of an unbranched peglike lateral branch
Z. insidians, p. 692
- Capturing organ consisting of an unbranched peglike lateral branch
from which arise apically from one to five long slender tentacles *Z. tentaculum*, p. 695

ZOOPHAGUS INSIDIANS Sommerstorff

Oesterr. botan. Zeitschr., 61:372, pls. 5-6. 1911

(Figure 67 A-G, p. 694)

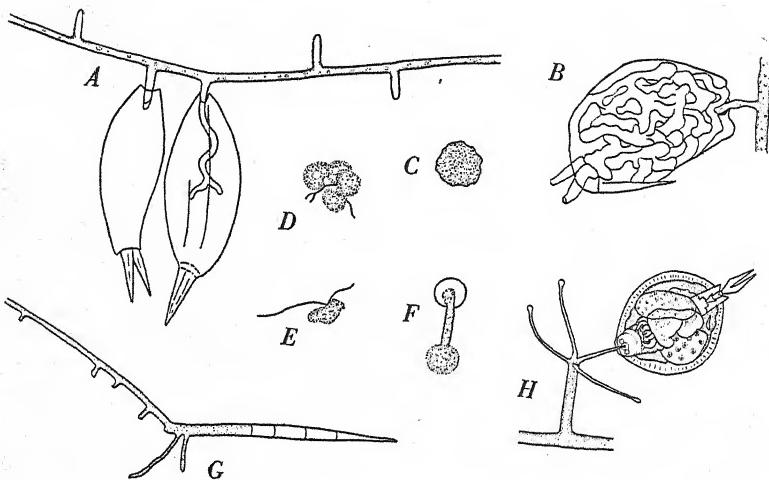
Mycelium slender, the main hyphae 6-7 μ in diameter, sparingly branched, frequently ramifying between and upon algae, forming numerous lateral unbranched spinelike or peglike apically refractive

capturing organs about 20μ long by 3μ in diameter which arise at right angles from the main hyphae, with which they are continuous, fusiform nonseptate or septate gemmae sometimes formed; zoosporangium consisting of an undifferentiated portion of the mycelium and an evacuation tube through which the amorphous contents are discharged into a vesicle, where the biflagellate zoospores mature; oögonium spherical, terminal on a lateral branch, brownish at maturity, antheridium single, terminal, clavate, diclinous; oöspore single.

A predaceous parasite of fresh-water rotifers. Sommerstorff (*loc. cit.*), Gicklhorn (1922), AUSTRIA; Gicklhorn (*op. cit.*), JUGOSLAVIA; Mirande (1920:figs. 1-2), FRANCE; Arnaudow (1921:figs. 1-8; 1925:figs. 1-5; 1936), Valkanov (1931b; 1931c; 1932:fig. 10), BULGARIA; Sparrow (1929; 1932b:pl. 8, fig. h; 1933c), Karling (1936c), UNITED STATES; Barnes and Melville (1932:94), Sparrow (1936a: 465), ENGLAND.

The description above is drawn mainly from the accounts of Sommerstorff (*loc. cit.*) and Arnaudow (1921, 1925). A comparison of the descriptions of zoospore formation in this species as given by Arnaudow (1921) and Gicklhorn (1922) shows quite clearly that two different fungi were involved, one (Arnaudow's) with a filamentous sporangium and the other (Gicklhorn's) with a globular or saccate sporangium. Both produced biflagellate zoospores, but in Gicklhorn's material the zoospores appeared to be formed in the sporangium before discharge, whereas they were matured outside the sporangium in Arnaudow's fungus. A study of the second account by Arnaudow (1925) of *Zoophagus insidians*, derived from material collected in Germany rather than Bulgaria, and the description of *Z. tentaculum* by Karling (1936c) reveals a striking similarity between the two fungi with respect to the method of formation and the shape of the conidia or "gemmae." Furthermore, Karling states that he was unable to obtain zoospore formation, and Arnaudow reports finding it in only one instance in the German material. From these considerations the interesting possibility arises that Karling and Arnaudow (German material) may be dealing with conidial Phycomyces.¹ Gicklhorn's fungus is quite certainly distinct from Arnaudow's Bulgarian material. Then, too, Gicklhorn's

¹ The presence of gemmae in Arnaudow's Bulgarian material, where zoospores were also found, would seem, however, to argue against this.

FIG. 67. *Zoophagus*

A-G. Zoophagus insidians Sommerstorff ($\times 250$), capturer of rotifers: *A*, portion of mycelium with short peglike lateral branches modified for capture of rotifers; two captured animals are shown in outline form; *B*, dead rotifer within which is a complex of hyphae which have become transformed into zoosporangia and have discharged their zoospores; *C*, discharged mass of protoplasm about to undergo cleavage into zoospores; *D*, zoospores undergoing cleavage; *E*, single zoospore; *F*, encysted zoospore undergoing repeated emergence; *G*, germinating septate gemma from which new mycelia are forming. *H. Zoophagus tentaculum* Karling, lateral branch with three capturing tenacles, to one of which a rotifer is attached.

(*A*, Sparrow, 1932b; *B-F*, Arnaudow, 1921; *G*, after Arnaudow, 1925; *H*, Karling, 1936c)

Plate 2, Figure F, presents structures which he regarded as "conidia," but which most certainly are encysted zoospores, clumped, as in *Sommerstorffia* and *Aphanomyces*, at the tip of a discharge tube projecting from the carapace of the rotifer. It is possible, therefore, that there exist several distinct fungi, alike in their vegetative stage and capturing organs, but differing in their nonsexual reproductive structures. Which character was typical of Sommerstorff's *Z. insidians* cannot now be determined with certainty, although from his few remarks concerning this phase of his fungus it is probable that zoospores were formed as they are in *Pythium*.

ZOOPHAGUS TENTACLUM Karling

Mycologia, 28:308, figs. 1-5. 1936

(Figure 67 H)

"Mycelium filamentous, greatly extended, 3-6 μ in diameter, hyaline, branched and continuous; possessing numerous relatively short specialized lateral branches, 15-35 μ in length and 3-5 μ in diameter, which bear one to five tenuous, predacious tentacles at the apex. Cytoplasm in the tips of the short lateral hyphae highly refractive; tentacles, 10-17 μ in length and 1.5 to 2 μ in diameter, and terminated by a small knob. Conidia or gemmae produced at the end of the long hyphae in acropetal succession, 40-80 μ in length and 3-6.5 μ in diameter. Growing loosely epiphytic on *Nitella flexilis*; predacious and parasitic on species of *Monostyla*, *Diostyla*, etc." (Karling, *loc. cit.*).

UNITED STATES.

PYTHIOGETON MINDEN

Falck, Mykolog. Untersuch. Berichte, 2 (2):241. 1916

(Figure 68, p. 698)

Mycelium well developed, consisting of delicate much-branched hyphae, appressoria occasionally formed; zoosporangium terminal or intercalary on the ordinary elements of the mycelium or on richly branched lateral hyphae, spherical or more commonly unsymmetrical and bursiform, the long axis often nearly at right angles to that of the concomitant hypha, forming a more or less prolonged slender evacuation tube, internally proliferous; zoospores somewhat reniform, each bearing a single vacuole and with two oppositely directed flagella of approximately equal length emerging from a shallow longitudinal groove, expelled from the sporangium as an undifferentiated irregularly tubular mass surrounded by an elongate quickly evanescent vesicle, undergoing their maturation free in the water, capable of repeated emergence; hyphae bearing the sex organs often helically involved; oögonium terminal or intercalary, spherical or polygonal, antheridium usually single, terminal or with a short appendage, arising (always?) from the same hypha as the oögonium; oöspore spherical, filling the oögonium, with an

enormously thickened refractive often concentrically layered wall and a large globule, upon germination converted (always?) into a zoosporangium after resorption of the greater part of the wall.

Saprophytic on vegetable debris in fresh water.

Because of the lack of essential data in Minden's descriptions and of the variations in shape and position of the zoosporangia his species are difficult to distinguish on the basis of the sporangial stage alone. A study of Minden's illustrations of his species, which are presumed to represent typical material, reveals the following qualitative differences between them. The sporangia of *Pythiogeton utriforme* and *P. ramosum* are predominantly terminal. Those of *P. transversum* are usually (but not always) intercalary, the distal part of the hypha often appearing as a slender appendage near the orifice of discharged sporangia. The sporangia of *P. utriforme* are somewhat more broadly pouchlike, their discharge tubes are more nearly in line with the mycelial axis, and they are borne on a more sparingly branched mycelium than are the narrowly bursiform ones of *P. ramosum*.

Sexual stages have been associated with *Pythiogeton utriforme* and *P. transversum*.

Species of the genus are as yet poorly defined in the literature, and further work will be necessary before taxonomic criteria of significant import can be established. Evaluation of the shape of the sporangium and of the sizes of the parts as characters of diagnostic importance—the primary bases on which all but two species of the genus are now separated—awaits the results of extensive studies of fungi identifiable with Minden's species as well as of those described since his time.

KEY TO THE SPECIES OF PYTHIOGETON

Sporangia bursiform or irregularly saccate

Sporangia for the most part terminal

Sporangia predominantly broadly bursiform, the discharge tube nearly parallel with the axis of the attendant hypha; sporangiferous hyphae sparingly branched; oögonia spherical *P. utriforme*, p. 697

Sporangia predominantly narrowly bursiform, the discharge tube approximately at right angles to the axis of the attendant hypha; sporangiferous hyphae richly branched; sex organs unknown *P. ramosum*, p. 699

Sporangia for the most part intercalary

Sporangia (four) averaging 154 μ long by 60.5 μ in diameter;
oögonia polygonal *P. transversum*, p. 699

Sporangia (one hundred) averaging 96 μ long by 42 μ in
greatest diameter; sex organs unknown ... *P. autossytum*, p. 700

Sporangia spherical or ovoid

Sporangia 40–56 \times 30–40 μ ; discharge tube 39–70 μ long

P. uniforme, p. 701

Sporangia 20–34 \times 18–28 μ ; discharge tube 4.8–15 μ long

P. dichotomum, p. 702

PYTHIOGETON UTRIFORME Minden

Falck, Mykolog. Untersuch. Berichte, 2 (2):242, pl. 6, figs. 56–65. 1916

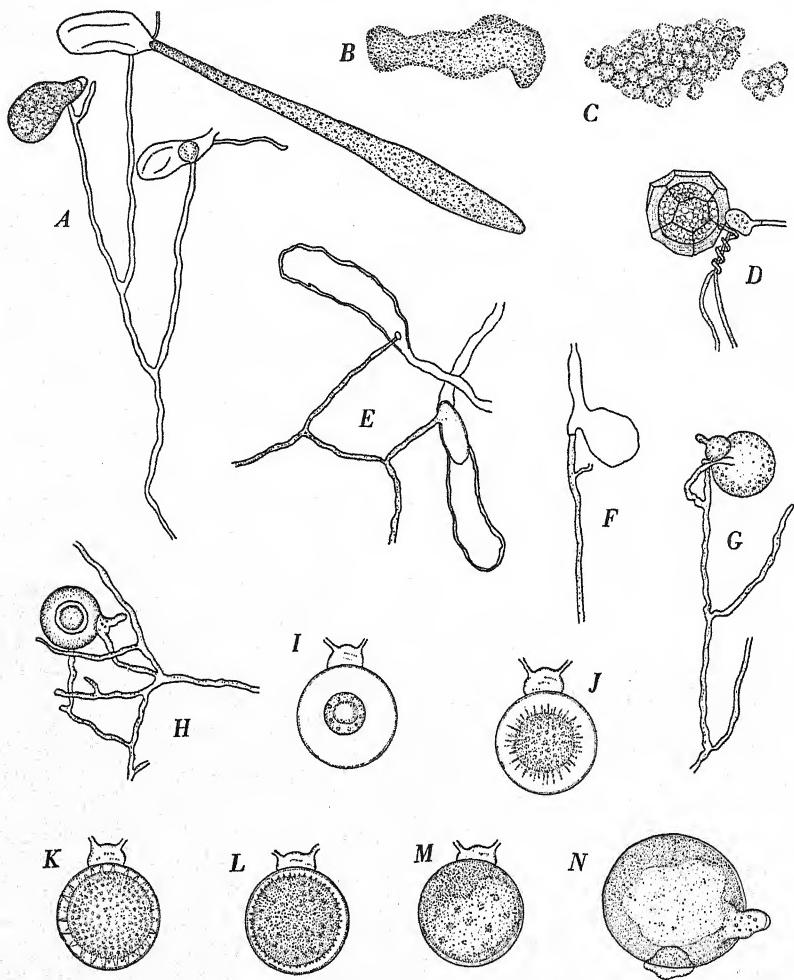
(Figure 68 F–M, p. 698)

Mycelium composed of slender sparingly branched hyphae 2.5–3.5 μ in diameter; zoosporangium terminal, bursiform or somewhat irregular, the discharge tube slender, more or less prolonged, its long axis frequently nearly parallel with that of the supporting hypha; zoospores reniform, laterally biflagellate; oögonium predominantly spherical, averaging 45 μ in diameter, antheridium single, monoclinous, hemispherical, sometimes bearing a short appendage, applied laterally or near the base of the oögonium, forming a fertilization tube; oöspore spherical, completely filling the oögonium, with a very thick refractive sometimes concentrically layered wall, contents bearing a single large globule surrounded by many small ones, upon germination converted (always?) into a zoosporangium after resorption of the greater part of the wall.

Saprophytic on fruits and twigs, Minden (*loc. cit.*), GERMANY; Thaxter (1895b: pl. 31, fig. 16, oöspore), UNITED STATES; Lund (1934:53, fig. 27), DENMARK; Sparrow (1936a:467, fig. 6 c, o–r, fig. 7 a–k), ENGLAND.

Minden has stated that this species may well be identical with the imperfectly described *Pythium utriforme* of Cornu (1872a:13). The resting spore suggested by Thaxter (*loc. cit.*) as belonging to *Gonapodya* is unquestionably that of the present species.

No measurements of the zoosporangia were given by Minden. The zoosporangia have been described by Lund (*loc. cit.*) as 45–97 \times 31–67 μ , the discharge tube as 49–63 μ long. In the material studied by Sparrow (*loc. cit.*) the zoosporangia were 32–45 μ long by 17–30 μ

FIG. 68. *Pythiogeton*

A-D. *Pythiogeton transversum* Minden: A, group of sporangia, one of which is discharging its contents; B, ejected contents free in the water; C, contents becoming segregated into zoospores; D, sex organs. E. *Pythiogeton ramosum* Minden, two empty sporangia. F-N. *Pythiogeton utriforme* Minden: F, empty sporangium; G, developing sex organs; H, mature oospore; I, mature oospore with persistent antheridium; J, beginning of germination; K-M, further stages in resorption of oospore wall; N, formation of discharge tube by germinating oospore. (I-N, $\times 400$).
 (A-H, Minden, 1916; I-N, Sparrow, 1936a)

in greatest diameter. The oögonia in Lund's material were, when spherical, $28\text{--}57 \mu$ in diameter, when subspherical, $34 \times 36 \mu$; the oöspores were $16\text{--}39 \mu$ in diameter.

Pythiogeton ramosum Minden

Falck, Mykolog. Untersuch. Berichte, 2 (2):238, pl. 8, figs. 74-(?)75. 1916
(Figure 68 E)

Mycelium composed of occasionally branched main hyphae bearing numerous secondary branches, on which the zoosporangia are formed; zoosporangium terminal, narrowly bursiform, its long axis at right angles to that of the supporting hypha, the narrow apex usually extended, internally proliferous; zoospores reniform, laterally biflagellate; sex organs unknown.

On decaying beet root, Minden (*loc. cit.*), GERMANY; rice seeds and seedlings, Ito and Nagai (1931:48), JAPAN; twigs, Sparrow (1932b:299, pl. 8, fig. I), UNITED STATES; Sparrow (*loc. cit.*), CANADA.

No dimensions were given by Minden. The species was considered doubtfully distinct from *Pythiogeton transversum*, the complex of branched sporangiferous hyphae being the chief point of difference. The sporangium, however, appears more narrowly bursiform than in typical *P. transversum*. The sporangia in Sparrow's material were about 60μ long and tapered from 20μ to 8μ in diameter.

Pythiogeton transversum Minden

Falck, Mykolog. Untersuch. Berichte, 2 (2):242, pl. 7, figs. 66-72. 1916
(Figure 68 A-D)

Mycelium composed of slender moderately branched hyphae; zoosporangium usually intercalary, placed near the tip of the hypha, which appears as a somewhat evanescent short appendage, irregularly bursiform, occasionally somewhat spherical, $70\text{--}299 \mu$ long (without including the discharge tube) by $42\text{--}79 \mu$ in diameter, the long axis usually nearly at right angles to that of the supporting hypha, to which it is attached near the narrower end, discharge tube more or less prolonged; zoospores reniform, laterally biflagellate; oögonium terminal or intercalary, at maturity polygonal, $37\text{--}51 \mu$ in diameter (averaging 50μ), antheridium single, androgynous, frequently helically involved by or involving the supporting

hypha of the oögonium, intercalary, placed near the tip of the hypha, which appears as a somewhat evanescent short appendage, applied near the base of the oögonium; oöspore spherical, nearly filling the oögonium, $33-50 \mu$ in diameter, with a thick refractive somewhat yellowish wall, contents bearing a large oil globule, germination not observed.

On various fruits and on stalks of water hemlock, Minden (*loc. cit.*), GERMANY.

In its globose sporangia a fungus referred to this species by Sparrow (1933c:533, pl. 49, fig. 24) more nearly resembles *Pythiogeton uniforme* Lund. As may be seen, Minden considered the intercalary forms with somewhat spherical sporangia indistinguishable specifically from the bursiform types.

PYTHIOGETON AUTOSSYTUM Drechsler

J. Wash. Acad. Sci., 22:447, figs. 1-5. 1932

"Intramatrical mycelium composed of hyphae branching mostly at rather wide angles and at moderate intervals, measuring 1.6 to 7.0μ in diameter, each element maintaining usually a nearly uniform width from origin to tip, the wider axial hyphae of straightforward course, the shorter branches usually with somewhat abrupt changes in direction, and often bearing appressoria in groups of 5 to 10 or more; the individual appressorium distended clavate, mostly 10 to 13μ in diameter and 20 to 30μ in length, after functional frustration often growing out into irregular processes of somewhat crescentic parts. Under aquatic condition extramatrical mycelium rather meager. Aerial mycelium on dry substrata generally meager, arachnoid, yet often spreading rather extensively over surfaces of adjacent bodies.

"Sporangium terminal or intercalary, when intercalary mostly borne only a short distance from the tip of the supporting filament, the distal element mostly 3 to 30μ in length remaining as an empty appendage; when produced under conditions suitable for zoospore production sometimes subspherical or ellipsoidal, but more often markedly ventricose, utriform, or bursiform, with the expanded part free and its axis directed athwart the axis of supporting hypha, or occasionally bilocular as through fusion of two parts, either of which

may be subspherical or bursiform; measuring 16 to 226 μ , mostly 50 to 150 μ (average 96 μ) in length and 13 to 68 μ , mostly 30 to 54 μ (average 42 μ) in greatest diameter; when formed under conditions unsuitable for zoospore formation, mostly subspherical measuring usually 32 to 51 μ (average 40.4 μ) in diameter. Evacuation tube arising often from position opposite attachment of supporting filament and directed in approximate alignment with that filament, but at other times originating from other positions; measuring mostly 3.5 to 7.0 μ (average between 5.5 and 6.0 μ) in diameter, and 5 to 300 μ in length; in cases of frustration often becoming septate, and discharging from a branch. Zoospores formed up to approximately 100 from a single sporangium, broadly reniform, the longitudinal furrow bearing the two cilia well-marked, the forward end more pointed than the rounded rear end, measuring mostly 18 to 20 μ in length and 11 to 13 μ in width in motile state; after rounding up measuring mostly 13 to 17 μ (average 15 μ) in diameter; germinating individually by the production of 1 to 4 delicate germ tubes, or giving rise to a secondary zoospore after proliferating an evacuation tube approximately 2 μ in diameter, and 2 to 27 μ in length" (Drechsler, *loc. cit.*).

On dying and decaying leaves of *Typha latifolia*, UNITED STATES.

PYTHIOGETON UNIFORME Lund

Kgl. Danske Vidensk. Selsk. Skrift., Naturv. Math., Afd. IX, 6(1):54, fig. 28 a-c. 1934

"Hyphae about 3-5 μ thick, much branched, sometimes divided by septa. Sporangia subspherical or slightly oval, 40-56 \times 30-40 μ , terminating the main hyphae or on side branches, mostly with their long axis at nearly right angles to the hyphae, filled with a granulated plasma. Tube of discharge about 39-70 \times 5.6 μ , filled with refractive plasma when young. At maturity the plasma of the sporangium passes through the tube of discharge as a long flowing stream; after some time about 20 biciliate zoospores are differentiated. When the sporangium has emptied, the walls collapse; proliferations frequent. Sexual organs not observed" (Lund, *loc. cit.*).

On hempseed in water, DENMARK.

PYTHIOGETON DICHOTOMUM Tokunaga

Trans. Sapporo Nat. Hist. Soc., 14 (1): 12. 1935

Mycelium intra- and extramatrical, hyphae branched, hyaline, slender, 1.8–3 μ in diameter; zoosporangium terminal on lateral branches, which are unbranched or once or twice dichotomously branched, spherical or ovoid, 20–34 \times 18–28 μ , proliferous, with an apical or lateral short exit tube, 4.8–15 μ long by 4–6 μ wide; vesicle oblong-ovoid, with an extremely delicate wall; zoospores reniform, with two lateral flagella; oögonium and oöspore unknown.

In decaying plants of *Oryza sativa*, JAPAN.

PYTHIOMORPHA H. E. PETERSEN

Bot. Tidsskrift, 29:391. 1909; Ann. Mycologici, 8:528. 1910. Emend.
Kanouse, Bot. Gaz., 79:198. 1925

(Figure 69 A–E, p. 704)

Mycelium much branched subdichotomously, the purely vegetative part bearing groups of irregular budlike outgrowths or involved torulose complexes, protoplasm strongly refractive, pallid, bearing occasional conspicuous granules (cellulin?), walls giving a cellulose reaction; zoosporangium borne on a slender unbranched or occasionally branched sporangiophore, ovoid, ellipsoidal, citriform, or somewhat pyriform, with a broad blunt papillate apex, proliferous, the secondarily formed sporangia either sessile and "nested" within the primary or borne on a sporangiophore which extends through the discharge orifice to the outside; zoospores of the secondary, laterally biflagellate, type, emerging fully formed from the sporangium, sometimes surrounded by a quickly evanescent vesicle, capable of repeated emergence; sexual reproduction oögamous, oöspore thick-walled, sometimes developed parthenogenetically, upon germination forming one or more germ tubes which reëstablish the thallus.

Saprophytic on vegetable debris in fresh water. Two species (*Pythiomorpha Miyabeana* and *P. Oryzae*) have been found to cause disease of seeds and seedlings in rice fields.

A discussion of the controversial features of this genus¹ and particularly of the type species *Pythiomorpha gonapodyides* has already been given (pp. 679, 689). Further investigation will be neces-

¹ See Blackwell and Waterhouse, *Mycologia*, 33:449. 1941; Blackwell, Waterhouse, and Thompson, *Trans. Brit. Mycol. Soc.*, 25:148. 1941.

sary to determine the precise limits of the genus, whether or not it is to be maintained separate from *Phytophthora*, how much weight is to be accorded the variations in sporangial discharge recorded in the various species of "Pythiomorpha," and how tenable are the species which have been referred to it. No critical treatment of *Pythiomorpha* can be attempted, therefore, at this time. In Figure 69 the types of sexual organs of *Pythiomorpha gonapodyoides* as figured by Kanouse (Fig. C), Cejp (Fig. D), and Forbes (Fig. E) are shown. In the same figure are represented (Figs. F-H) the zoosporangia and sex organs of *Phytophthora megasperma* as figured by Drechsler.

KEY TO THE SPECIES OF PYTHIOMORPHA

Oögonia and antheridia present; sporangia renewed by internal proliferation as well as by cymose branching of the supporting hyphae

Hyphae not strongly undulate

Sporangiophore unbranched; sex organs present

Antheridium diclinous; oöspore filling oögonium, without a reserve globule *P. gonapodyoides*, p. 703

Antheridium androgynous; oöspore not filling oögonium, bearing a large reserve globule *P. Miyabeana*, p. 705

Sporangiophore branched; sex organs lacking *P. Oryzae*, p. 706

Hyphae strongly undulate *P. undulata*, p. 707

Oögonia, only, formed; sporangia renewed only by cymose branching *P. Fischeriana*, p. 707

PYTHIOMORPHA GONAPODYOIDES H. E. Petersen

Bot. Tidsskrift, 29:391, figs. 6-7. 1909; Ann. Mycologici, 8:528, figs. 6-7. 1910. Emend. Kanouse, Bot. Gaz., 79:198, pls. 12-13. 1925

(Figure 69 A-D, p. 704)

Phytophthora gonapodyoides (H. E. Petersen) Buismann, Root Rots Caused by Phycomycetes, p. 7. Haarlem, 1927.

Mycelium delicate, profusely branched, with a silvery sheen, the hyphae irregular, 2-8 μ in diameter, bearing budlike projections and knotted complexes, endobiotic and extramatrical, contents with occasional refractive granules; zoosporangium borne on a slender unbranched sporangiophore about 3 μ in diameter, ovoid or pyriform with a broad apical papilla which may disappear just prior to zoospore discharge, 26-48 μ long by 16-27 μ in diameter, inner wall distinct, renewed by internal proliferation, the secondarily formed sporangia

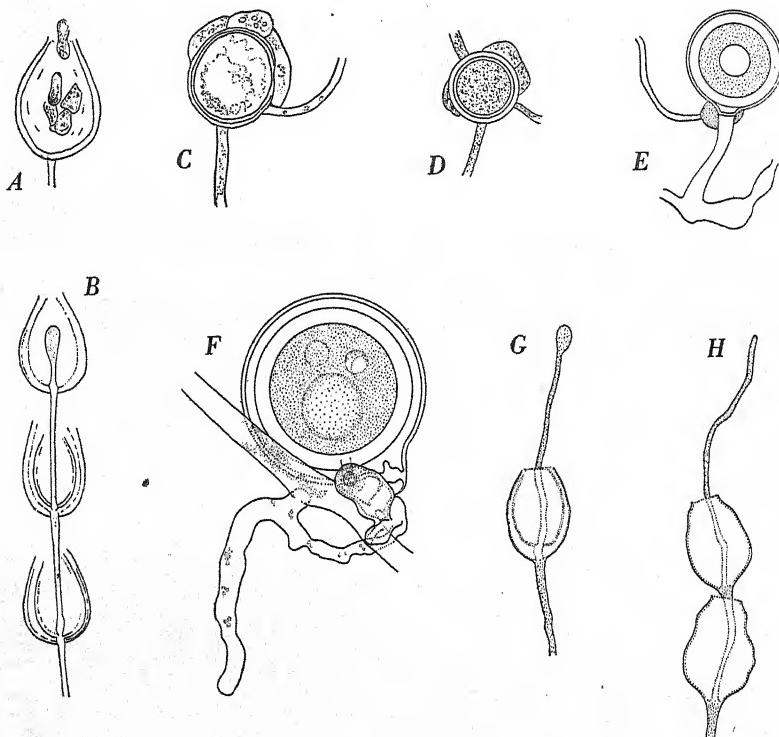


FIG. 69. *Pythiomorpha* and *Phytophthora*

A-E. Pythiomorpha gonapodyides H. E. Petersen: *A*, fully formed zoospores emerging from a sporangium; *B*, series of proliferous zoosporangia; *C*, sex organs figured by Kanouse; *D*, sex organs figured by Cejp; *E*, sex organs figured by Forbes. *F-H. Phytophthora megasperma* Drechsler: *F*, sex organs figured by Drechsler ($\times 500$); *G-H*, proliferous sporangia ($\times 250$). (See p. 679 in regard to present status of *Pythiomorpha*.)

(*A-C*, Kanouse, 1925; *D*, Cejp, 1933b; *E*, Forbes, 1935a; *F-H*, Drechsler, 1931)

up to five in number, either sessile and "nested" within the primary sporangia or formed in linear succession by repeated apical growth of the sporangiophore through the base of the sporangium; zoospores formed and initiating movement within the sporangium, somewhat ovoid, 9–15 μ in diameter, the flagella of about equal length, oppositely directed and arising from a shallow groove, capable of re-

peated emergence, upon germination forming one or more germ tubes; oögonium formed on a short branch, spherical, smooth-walled, $22-36 \mu$ in diameter, antheridium present on about ten per cent of the oögonia, dichlinous, somewhat clavate, broadly applied to the oögonium, the antheridial hypha winding around the oögonium; oöspore smooth, thick-walled, filling the oögonium, contents highly refractive, finely granular, without a conspicuous globule, upon germination forming one or more branched hyphae.

Saprophytic on fruits and twigs, Petersen (*loc. cit.*), Lund (1934: 47), DENMARK; (?) fruits and other plant parts, Minden (1916:219, text fig. 24, pl. 6, figs. 45-48), Cejp (1933b: pl. 1, figs. 1-18, pl. 2), GERMANY; fruits, Kanouse (*loc. cit.*), *Fraxinus* twigs, Sparrow (1933c:533), UNITED STATES; Barnes and Melville (1932), twigs, Sparrow (1936a:467), (?) Forbes (1935a: pl. 9, fig. 7), ENGLAND; fruits, Crooks (1937:220, fig. 6 A-E), AUSTRALIA.

The description above was derived for the most part from Miss Kanouse's account of her fungus. The fungi described by Cejp (*op. cit.*) and Miss Crooks (*op. cit.*) most nearly approximate it, particularly with respect to the sex organs and the oöspore. The sporangia of the Australian material were, however, somewhat larger, being $40-70 \times 20-40 \mu$. The oögonia were $23-28 \mu$ in diameter, and the oöspores, which lacked a globule and filled the oögonium, were $20-22 \mu$ in diameter. It is possible that larger sporangia were also formed in the material described by Cejp. The statement has been made (Kanouse, *loc. cit.*) that the oöspore resting in the oögnoum is surrounded by three walls. From the figures given it appears more likely that this is a misinterpretation due to the fact that the oögonial wall is as thick as that of the oöspore.

PYTHIOMORPHA MIYABEANA Ito and Nagai

J. Fac. Agr. Hokkaido Imper. Univ., Sapporo, 32:50, pl. 8, figs. 1-8. 1931

"Mycelia extra- and intra-matrical; hyphae non-septate, often more or less swollen in knob-like appearance at irregular intervals, $2.5-4.8 \mu$, mostly $3-3.5 \mu$ in width. Sporangia lemon-shaped, broadest at the base, $36-53 \times 17-36 \mu$ mostly $46-48 \times 24-29 \mu$ in size; later sporangia produced on the hyphae proliferated inwardly through the empty preceding ones. Zoospores ellipsoidal, $8.5-9.5 \mu$ in diameter, matured in the sporangium, swarming out directly.

Oogonial stalks recurved or coiling, developed laterally on the main hyphae. Oogonia abundant, globular, dark yellowish at maturity, $28\text{--}50.5\ \mu$ in diam., with an oospore; wall smooth, thin, unpitted, about $1.8\ \mu$ thick. Antheridial branches short, usually arising androgynously from the main hyphae or from the oogonial stalks. Antheridia clavate or oblong, attached by the apices to the oogonial wall. Oospores globular, smooth, $24\text{--}36\ \mu$ in diam. Gemmae globular or somewhat irregular in shape, intercalary, nearly equal to the oogonia in size" (Ito and Nagai, *loc. cit.*).

On seeds and seedlings in rice fields, JAPAN.

Pythiomorpha Miyabeana and *P. Oryzae* are included in the present discussion because of the distinctly aquatic conditions prevailing in rice fields and because of the strong possibility that they also exist saprophytically in the water.

Pythiomorpha "Sp. III" of Lund (1934:50, fig. 24 d-e), on twigs of *Alnus*, Denmark, may perhaps be referable to this species.

PYTHIOMORPHA ORYZAE Ito and Nagai

J. Fac. Agr. Hokkaido Imper. Univ., Sapporo, 32:51, pl. 8, fig. 9, pl. 9, figs. 1-6. 1931

"Mycelia extra- and intra-matrical; hyphae non-septate, branched monopodially, often swollen in knob-like appearance at irregular intervals, $3.5\text{--}11\ \mu$ mostly $6\text{--}8\ \mu$ in width. Sporangia ovoid, ellipsoidal or somewhat elongated, $41\text{--}84 \times 26\text{--}48\ \mu$ mostly $60\text{--}84 \times 29\text{--}43\ \mu$ in size; later sporangia produced on the hyphae proliferated onwardly through the empty ones, or on the lateral branch from the base of them. Zoospores ellipsoidal or kidney-shaped, about $12 \times 7\ \mu$, matured in the sporangium, swarming out directly or discharged being wrapped with the vesicle-membrane which is soon broken off by the self-agitation of the zoospores, and then swarming away. Oogonia and antheridia absent. Gemmae globular or somewhat irregular in shape, intercalary. Hyphal clumps produced on corn-meal agar" (Ito and Nagai, *loc. cit.*).

On seedlings in rice fields, JAPAN.

Pythiomorpha "Sp. I" of Lund (1934:49, fig. 24 a-b) may possibly be referable to this species. It was found on twigs of *Salix* in Denmark.

PYTHIOMORPHA UNDULATA Apinis

Acta Horti Bot. Univ. Latv., 4:234, fig. 4. 1930

Mycelium sparingly branched, the hyphae 3–8 μ in diameter, often undulate, the walls stout, sometimes faintly golden or brownish; zoosporangium either terminal and borne at the tip of the main hypha or its branches or by cymose branching appearing lateral, narrowly ovoid, 45–167 μ long by 20–52 μ in diameter, with a prominent terminal papilla, proliferous, the secondary sporangia either sessile and "nested" within the primary one or borne on a strongly undulate sporangiophore which extends through the orifice to the outside; zoospores formed within the sporangium, 10–18 μ in diameter, with two lateral oppositely directed flagella, capable of repeated emergence; sexual reproduction not observed.

On plant parts, Apinis (*loc. cit.*), LATVIA; fruits and twigs, Lund (1934:48, fig. 23), DENMARK; plant debris, Cejp (1933b: pl. 1, figs. 19–21), GERMANY.

The species has been considered synonymous with *Pythium undulatum* Petersen by Sparrow (1932b:299). Apinis, on the other hand, believes his fungus to be the same as Petersen's and cites *Pythium undulatum* as a synonym. Lund (1934) has observed similar-appearing fungi, one of which produces zoospores as does *Pythium*, the other, as does *Pythiomorpha*. He concludes, therefore, that *Pythiomorpha undulata* and *Pythium undulatum* are two distinct fungi. At least three other observers (Dissmann, 1927; de Wildeman, 1931¹; Sparrow, *loc. cit.*) have confirmed the occurrence of the *Pythium* type of zoospore discharge in *Pythium undulatum*.

PYTHIOMORPHA FISCHERIANA Höhnk

Bot. Centralbl., 55 (Abt. A):92, fig. 2. 1936

Mycelium intra- and extramatrical, the intramatrical hyphae stout, constricted, and irregular, the extramatrical slender, 2–3 μ in diameter, regular; zoosporangium ovate, 28–46 μ in diameter, renewed by cymose branching of the sporangiophore; zoospores formed within the sporangium, discharged as individuals at the

¹ See also de Wildeman in *Travaux cryptogamiques dédiés à Louis Mangin* (Paris: Muséum national d'histoire naturelle, Laboratoire cryptogamie, 1931).

rupturing of its tip, at first irregular in shape but quickly becoming reniform, 10μ in diameter, with two lateral flagella; gemmae intercalary, ovoid, with thickened walls, rarely terminal and spherical; oögonium apogamous, at maturity bearing loosely within it a single egg with a thickened wall.

On *Alnus* twigs in water, GERMANY (and the UNITED STATES?).

LIST OF SUBSTRATA¹

PLANTS

Algae

Myxophyceae.—*Anabaena circinalis*: *Rhizophyllum cornutum*.—*A. Flos-aquae*: *Phlyctidium megastomum*.—*Calothrix* sp. (gelatinous sheath): *Coenomyces consuens*.—*C. (Mastigothrix) aeruginea*: *Rhizophlyctis Mastigotrichis*, *Rhizophyllum microsporum*.—*Chroococcus turgidus*: *Rhizophyllum agile*.—*Dicothrix (Schizosiphon) kerguelensis*: *Rhizophyllum caudatum*.—*Filarszkya* sp.: *Rhizosiphon crassum*.—*Hormotheca sicula*: *Nowakowskia Hormothecae*.—*Lyngbya Aestuarii* (filaments): *Resticularia nodosa*.—*Lyngbya* sp.: *Rhizophyllum megarrhizum*.—*Oscillatoria tenuis* var. *subfusca*: *Rhizophyllum subangulosum*.—*Oscillatoria* sp.: *Phlyctidium anatropum*.—“*Oscillatoriens*”: *Rhizophyllum megarrhizum*.—*Oscillatoria* sp.: *Rhizophyllum megarrhizum*, *R. subangulosum*.—*Tolypothrix lanata*: *Rhizophlyctis Tolypotrichis*.—*Tolypothrix* sp.: *Resticularia Boodleai*, *R. nodosa*.

Chlorophyceae.—*Apiocystis Brauniana*: *Rhizophyllum Brauni*.—*Bryopsis plumosa*: *Sirolpidium Bryopsidis*, *Thraustochytrium proliferum*.—*Bulbochaete setigera* (setae): *Chytridium minus*.—*Bulbochaete* sp. (setae): *Chytridium chaetophilum*, *C. Schenckii*.—*Chaetomorpha* sp.: *Lagenidium* sp.—*Chaetophora elegans* (gelatinous sheath): *Amoebochytrium rhizidioides*.—*C. elegans*: *Phlyctidium anatropum*.—*C. elegans* (gelatinous sheath): *Rhizidium mycophilum*.—*Chaetophora* sp. (gelatinous sheath): *Nowakowskia elegans*.—*Characium* sp.: *Chytridium (?) Characi*.—*Chlamydomonas Dillii*: *Rhizophyllum transversum*.—*C. globulosa*: *Rhizidiozymes Ichneumon*.—*C. obtusa*: *Rhizophyllum transversum*.—*C. pluvialis*: *Polyphagus Nowakowskii*.—*C. pulvisculus*: *Entophysycis apiculata*, *Rhizophyllum transversum*.—*C. Reinhardi*: *Polyphagus Euglenae*.—*Chlamydomonas* sp.: *Entophysycis apiculata*, *Polyphagus Euglenae*, *P. Euglenae* var. *minor*, *Rhizophyllum aciforme*, *R. vernale*, *Scherffeliomyces appendiculatus*.—*Chlorococcum (?)*: *Rhizophyllum simplex*.—*Chlorogonium eu-chlorum*: *Phlyctidium Chlorogonii*.—*Cladophora fracta*: *Chytridium gibbosum*.—*C. glomerata*: *Catenaria sphaerocarpa*, *Entophysycis Confervae-glo-meratae*, *E. maxima*, *Olpidium entophytum*, *Rhizophyllum macrosporum*.—*C. (Acrosiphonia) hystric*: *Olpidiopsis Andreei*.—*C. (Acrosiphonia) incurva*: *Olpidiopsis Andreei*, *Rhizophyllum discinctum*.—*C. Kuttingiana*: *Myzocytium proliferum*.—*C. (Acrosiphonia) pallida*: *Rhizophyllum gelatinosum*.

¹ Usually the host binomial cited is that which appears in the original paper. The substratum is given first; the fungus or fungi inhabiting it follow the colon.

—*Cladophora* sp.: *Achlyogeton entophytum*.—*Cladophora* sp. (marine): *Achlyogeton salinum*.—*Cladophora* sp.: *Bicrictium transversum*, *Catenaria sphaerocarpa*, *Chytridium aggregatum*, *C. inflatum*, *C. Lagenaria*, *C. Schenkii*, *Diplophlyctis laevis*, *Endochytrium ramosum*, *Entophlyctis Confervae-gloemeratae*, *Myzocytium proliferum*.—*Cladophora* (*Acrosiphonia*) sp. (marine): *Olpidiopsis Andreei*.—*Cladophora* sp. (marine): *Olpidium aggregatum*.—*Cladophora* sp.: *Olpidium entophytum*, *Phlyctidium spinulosum*, *Phlyctochytrium bullatum*, *P. chaetiferum*, *P. dentiferum*, *P. planicorne*, *P. quadricorne*, *P. urceolare*, *Rhizophydium ampullaceum*, *R. chaetiferum*, *R. messanense*, *Saccopodium gracile*.—*Cladophora* sp. (marine): *Siroldium Bryopsidis*.—*Coleochaete prostrata*: *Chytridium depressum*.—*C. pulvinata* (oögonia): *Rhizophydium Coleochaetes*.—*C. pulvinata*: *Rhizophydium mammillatum*.—*C. scutata*: *Phlyctidium Brebissonii*.—*Coleochaete* sp.: *Cladochytrium replicatum*.—*Draparnaldia glomerata*: *Pseudolpidium (?) deformans*, *Rhizophydium mammillatum*, *Sporophlyctis rostrata*.—*D. nudiuscula*: *Rhizophydium mammillatum*.—*D. plumosa*: *Sporophlyctis rostrata*.—*Draparnaldia* sp.: *Rhizophydium mammillatum*.—*Eudorina elegans*: *Endocoenobium Eudorinae*, *Phlyctidium Eudorinae*, *Rhizophydium Eudorinae*.—*E. illinoiensis*: *Phlyctidium Eudorinae*.—*Eudorina* sp.: *Phlyctidium Eudorinae*.—*Gloeococcus* (*Chlamydomonas* ?) *mucosus*: *Entophlyctis apiculata*.—*Gloeocystis* sp.: *Entophlyctis apiculata*, *Rhizophydium digitatum*.—*Gonium tetras*: *Rhizophydium transversum*.—*Hormidium flaccidum*: *Rhizophydium Hormidii*.—*H. penicilliformis*: *Olpidium entosphaericum*.—*H. varium*: *Rhizophydium cornutum*.—*Hormiscia uniflexa*: *Rhizophydium Haynaldii*.—*H. zonata*: *Endolpidium* sp.—*Hormiscia* sp.: *Rhizophydium transversum*.—*Hydrodictyon reticulatum*: *Catenaria sphaerocarpa*, *Hypothecium Hydrodictii*, *Phlyctochytrium chaetiferum*, *P. Hydrodictyi*.—*H. utriculatum*: *Phlyctochytrium Hydrodictyi*.—*Oedogonium apophysatum* (oögonia): *Chytridium brevipes*.—*O. Bospii*: *Lagenidium syncytiorum*.—*O. capillare*: *Chytridium olla*.—*O. cardiacum*: *Rhizophydium decipiens*.—*O. crassusculum* var. *idiosporum*: *Rhizophydium ampullaceum*.—*O. crenulato-costatum*: *Rhizophydium ampullaceum*.—*O. echinospermum* (?): *Chytridium acuminatum*.—*O. echinospermum* (oögonia): *Rhizophydium decipiens*.—*O. flavescentes* (oögonia): *Chytridium brevipes*.—*O. plagiostomum*: *Rhizophydium ampullaceum*.—*O. plusisporum*: *Lagenidium Rabenhorstii*.—*O. rivulare*: *Phlyctochytrium quadricorne*, *Rhizophydium globosum*.—*O. Rothii* (oögonia): *Chytridium acuminatum*.—*O. rufescens*: *Rhizophydium decipiens*.—*O. sexangulare*: (?) *Rhizophydium decipiens*.—*O. tumidulum* (oögonia): (?) *Rhizophydium decipiens*.—*O. tumidulum*: *Rhizophydium globosum*.—*O. undulatum*: *Rhizophydium ampullaceum*.—*O. Vaucherii*: *Chytridium brevipes*, *Rhizophydium decipiens*.—*O. Vaucherii* (oögonia): *Rhizophydium sporocotonum*.—*O. vesicatum*: *Rhizophydium*

ampullaceum.—*Oedogonium* sp. (filaments, oögonia): *Aphanistis Oedogoniorum*.—*Oedogonium* sp.: *Aphanistis pellucida*, *Chytridium aggregatum*, *C. brevipes*, *C. chaetophilum*, *C. inflatum*, *C. Lagenaria*, *C. minus*, *C. Oedogonii*.—*Oedogonium* sp. (oögonia, oöspores): *Chytridium olla*.—*Oedogonium* sp. (oögonia, oöspores, vegetative cells): *Chytridium Schenckii*.—*Oedogonium* sp.: *Chytridium Schenckii*, *Cladochytrium replicatum*, *Entophyscystis bulligera*, *Lagenidium Marchalianum*, *L. Oedogonii*, *L. Zoppii*, *Myzocytium proliferum*, *Olpidiopsis Oedogoniarum*, *Olpidium indicum*, *O. pusillum*, *Phlyctidium brevipes*, *Phlyctochytrium biporusum*, *P. chaetiferum*, *P. Lagenaria*, *P. planicorne*, *Plasmophagus Oedogoniorum*, *Pleotrichelus Petersenii*, *Resticularia Oedogonii*, *Rhizophyllum ampullaceum*, *R. chaetiferum*, *R. decipiens*, *R. globosum*.—*Oedogonium* sp. (oögonia): *Rhizophyllum mammillatum*.—*Oedogonium* sp. (oöspore): *Rhizophyllum (?) setigerum*.—*Oedogonium* sp.: *Rhizophyllum sphaerocarpum*.—*Oedogonium* sp. (oögonia, oöspores): *Rhizophyllum v. Mindenii*.—*Oocystis solitaria* var. *Wittrockiana*: *Rhizophyllum pseudodistomum*.—*Palmodictyon* sp.: *Rhizophyllum acuiforme*.—*Pandorina morum*: *Phlyctochytrium Pandorinae*.—*P. morum* (nonsexual colonies): *Dangeardia mammillata*.—*Pandorina* sp.: *Rhizophyllum simplex*.—*Pithophora* sp.: *Catenaria sphaerocarpa*, *Rhizophyllum macrosporum*.—*Protoderma* sp.: *Sporophlyctidium africanum*.—*Rhizocladium hieroglyphicum*: *Chytridium Lagenaria*, *Phlyctochytrium Hydrodictyi*, *P. planicorne*.—*Sphaerella lacustris*: *Chytridium Chlamidococcus*.—*S. (Haematooccus) lacustris*: *Rhizidium vorax*.—*Sphaerella (Haematooccus)* sp.: *Chytridium Haematococci*.—*Sphaeroplea annulina*: *Rhizophyllum globosum*.—*Spongomerpha vernalis*: *Rhizophyllum discinctum*.—*Spongomerpha* sp.: *Olpidiopsis Andreei*.—*Stigeoclonium* sp.: *Chytridium curvatum*, *C. papillatum*, *C. sphaerocarpum*, *Olpidium Stigeoclonii*, *Phlyctidium anatropum*, *P. laterale*, *Rhizophyllum mammillatum*, *R. ovatum*.—*Ulothrix albicans* (?): *Chytridium minus*.—*U. zonata*: *Rhizophyllum Haynaldii*, *R. laterale*.—*Ulothrix* sp.: *Rhizophyllum globosum*.—*Vaucheria geminata*: *Chytridium pyriforme*, *Entophyscystis rhizina*, *E. Voronichinii*, *Olpidium entophysatum*.—*V. globifera* (salina ?): *Olpidium entophysatum*.—*V. polysperma*: *Phlyctochytrium quadricorne*.—*V. sessilis*: *Chytridium pyriforme*, *Entophyscystis rhizina*, *E. Vaucheriae*, *E. Voronichinii*.—*V. sessilis* (oögonia): *Latrostium comprimens*.—*V. sessilis*: *Olpidium entophysatum*.—*V. sessilis* (oögonia): *Rhizophyllum multiporum*, *R. Vaucheriae*.—*V. sessilis*: *Woronina glomerata*.—*V. terrestris* (oögonia): *Latrostium comprimens*.—*V. terrestris*: *Woronina glomerata*.—*Vaucheria* sp.: *Chytridium Lagenaria*, *C. Schenckii*, *Entophyscystis helioformis*, *Olpidium entophysatum*, *Phlyctochytrium biporusum*.—*Vaucheria* sp. (filaments): *Rhizophyllum Constantineani*.—*Vaucheria* sp. (ripe oöspores): *Rhizophyllum pyriformis*.—*Vaucheria* sp.: *Woronina glomerata*.—*Volvox globator*: *Chytridium volvocinum*.

Zygnematales.—*Mougeotia genuflexa*: Rhizophydium sphaerocarpum.—*M. parvula*: *Micromyces Zygogonii*, Rhizophydium sphaerocarpum, *Zygorhizidium Willei*.—*M. (Mesocarpus) pleurocarpa*: *Myzocytium proliferum*, *Phlyctidium minimum*.—*M. scalaris*: *Micromyces Zygogonii*, *Olpidium Mougeotia*.—*M. sphaerocarpa*: Rhizophydium sphaerocarpum.—*M. viridis*: Rhizophydium *Hormidii*.—*Mougeotia (Mesocarpus) sp.* (zygospores): Chytridium acuminatum.—*Mougeotia sp.*: Chytridium *Mesocarpi*, *C. sphaerocarpum*, *Entophyscylis bulligera*, *E. pygmaea*, *Lagenidium Rabenhorstii*, *Micromyces Petersenii*, *M. Zygogonii*, *Myzocytium proliferum*.—*Mougeotia (Mesocarpus) sp.*: *Olpidiopsis appendiculata*, *O. elliptica*.—*Mougeotia sp.* (vegetative cells, gametangia, rarely zygospores): *Olpidiopsis Schenkiana*.—*Mougeotia (Mesocarpus) sp.*: *Olpidium Mesocarpi*.—*Mougeotia sp.*: Rhizophydium ampullaceum, *R. Couchii*, *R. digitatum*, *R. fallax*, *R. sphaerocarpum*.—*Mougeotia (Gonatonema) sp.*: Rhizophydium sphaerocarpum.—*Mougeotia sp.*: *Zygorhizidium Willei*.—*Spirogyra affinis*: *Myzocytium proliferum*.—*S. areolata*: Rhizophydium *Couchii*.—*S. calospora*: *Lagenidium entophytum*.—*S. crassa*: *Catenaria sphaerocarpa*, Chytridium aggregatum, *Cladochytrium replicatum*, *Entophyscylis bulligera*, *E. Confervae-glomeratae*, *Phlyctochytrium Lagenaria*, *Rhizophydium rostellatum*.—*S. Grevilleana* (gametangia, zygospores): *Lagenidium gracile*.—*S. inflata*: *Micromyces Spirogyrae*.—*S. insignis*: *Lagenidium entophytum*, *Phlyctochytrium equale*.—*S. Jurgensii*: *Myzocytium proliferum*.—*S. longata*: *Olpidiopsis fibrillosa*, *Zygorhizidium Willei*.—*S. majuscula* (zygospores): *Blyttiomycetes spinulosus*.—*S. majuscula*: *Olpidium endogenum*.—*S. maxima*: *Myzocytium proliferum*.—*S. mirabilis*: *Myzocytium proliferum*.—*S. orthospira*: *Lagenidium Rabenhorstii*, *Phlyctochytrium dentatum*.—*S. quadrata*: *Micromyces Zygogonii*.—*S. Spreeiana*: *Phlyctochytrium equale*.—*S. varians*: *Lagenidium entophytum*.—*S. varians* (gametangia): *Phlyctidium brevipes*.—*S. varians*: *Phlyctochytrium planicorne*, *Rhizophydium minutum*.—*S. Weberi* (zygospores): *Blyttiomycetes spinulosus*.—*Spirogyra sp.* (zygospores): *Blyttiomycetes spinulosus*.—*Spirogyra sp.*: Chytridium *Kolianum*, *C. Lagenaria*, *C. Schenkii*, *C. sphaerocarpum*, *Endochytrium pseudodistomum*, *Entophyscylis Confervae-glomeratae*.—*Spirogyra (Rhynchonema) sp.*: *Entophyscylis tetraspora*.—*Spirogyra sp.*: *Entophyscylis Vaucheriae*, *Lagenidium entophytum*.—*Spirogyra sp.* (zygote, zygospores): *Lagenidium entophytum*.—*Spirogyra sp.* (gametangia, zygospores): *Lagenidium gracile*.—*Spirogyra sp.*: *Lagenidium papillosum*, *L. Rabenhorstii*, *Micromyces longispinosus*, *Micromycopsis cristata* var. *minor*, *Myzocytium proliferum*, *Olpidiopsis fibrillosa*.—*Spirogyra sp.* (vegetative cells, gametangia, zygospores): *Olpidiopsis Schenkiana*.—*Spirogyra sp.*: *Olpidiopsis Zoppii*, *Olpidium entophytum*, *Phlyctidium brevipes*, *P. olla*, *Phlyctochytrium biporusum*, *P. dentatum*, *P. Hallii*, *P. Lagenaria*, *P. laterale*, *P. planicorne*.—*Spirogyra sp.* (zygospores): *Phlyctochytrium Spirogyrae*.—*Spirogyra sp.*: *Phlyctochytrium stellatum*, "Rhizidium algaecolum," Rhizo-

phydium ampullaceum, R. Couchii, R. dubium, R. globosum, R. laterale, R. simplex, R. sphaerocarpum, Rhizophydium sp., Saccopodium gracile.—*Zygnema cruciatum*: Myzocytium proliferum, Phlyctochytrium Zygnetmatis.—*Z. stellinum*: Micromycopsis zygnaemicola, Phlyctochytrium Zygnetmatis.—*Zygnema* sp.: Chytridium Kolianum, C. Schenkii, C. sphaerocarpum, Coralliochytrium Scherffelii, Endochytrium pseudodistomum, Entophyscites bulligera, Lagenidium Rabenhorstii, Myzocytium proliferum, Olpidium zygnaemicola, Phlyctochytrium Lagenaria, P. stellatum, Rhizophydium Barkerianum, Zygorhizidium Willei.—*Zygomonium* sp.: Micromyces Zygomonii, Micromycopsis Fischerii.

Desmids (*placoderm and saccoderm*).—Arthrodeshmus sp.: Bicricium naso.—Closterium acerosum: Myzocytium megastomum, M. proliferum.—C. angustatum: Myzocytium proliferum.—C. areolatum: Myzocytium megastomum.—C. attenuatum: Myzocytium megastomum.—C. didymotocum: Myzocytium proliferum.—C. Ehrenbergii: Lagenidium intermedium, Phlyctochytrium Desmidiaeacearum.—C. lunula: Olpidium endogenum, Rhizophydium globosum.—C. rostratum: Lagenidium Closterii.—C. striolatum (?): Lagenidium Closterii.—Closterium sp.: Chytridium gibbosum, C. Schenkii, Lagenidium Closterii, Myzocytium megastomum, M. proliferum, Olpidium endogenum, O. rostratum, Rhizophydium globosum, R. septocarpoides, R. verrucosum.—Cosmarium Botrytis: Olpidium saccatum, O. utriculiforme.—C. connatum: Myzocytium proliferum.—C. didymochondrum: Myzocytium proliferum.—C. pachydermum: Olpidium endogenum.—Cosmarium sp.: Myzocytium irregulare, M. proliferum, Olpidium endogenum, O. immersum, O. saccatum, Phlyctochytrium Autrani.—Cylindrocystis Brebissonii: Zygorhizidium Willei.—Cylindrocystis sp.: Rhizophydium gibbosum.—Desmidium Swartzii: Olpidium entophytum.—Docidium Ehrenbergii: Mitochytridium ramosum.—Docidium sp.: Mitochytridium ramosum.—Euastrum humerosum: Lagenidium entophytum.—Euastrum sp.: Olpidium endogenum.—Genicularia sp.: Rhizophydium globosum.—Hyalotheca dissiliens: Micromycopsis cristata, Olpidium Hyalothecae, Rhizophydium Hyalothecae.—H. dubia: Micromycopsis cristata.—Micrasterias denticula: Myzocytium irregulare.—M. mahabuleshwarensis var. Wallichii: Lagenidium entophytum.—M. rotata: Myzocytium irregulare.—Micrasterias sp.: Myzocytium irregulare, Olpidium endogenum.—Netrium digitus: Phlyctochytrium Desmidiaeacearum.—Netrium sp.: Micromyces Zygomonii.—Penium digitus: Rhizophydium globosum.—Penium sp.: Olpidium endogenum, Rhizophydium gibbosum.—Phycastrum sp.: Rhizophydium gibbosum.—Pleurotaenium trabecula: Rhizophydium globosum.—Pleurotaenium sp.: Olpidium endogenum.—Sphaerozosma vertebratum: Olpidium algarum var. brevirostrum.—Spirotaenia condensata: Chytridium Spirotaeniae, Rhizophydium Spirotaeniae.—Spirotaenia sp.: Myzocytium megastomum, Rhizophydium globosum.—

Staurastum dejectum var. *de Baryanum* (zygote): *Chytridium muricatum*.—*Staurastrum* sp.: *Olpidium immersum*, *O. saccatum*, *Rhizophydiwm globosum*.—*Tetmemorus* sp.: *Olpidium endogenum*.—"Desmid" (zygote): *Chytridium* sp.—"Desmids": *Olpidium endogenum*, *O. immersum*, *O. saccatum*, *O. utriculiforme*, *Rhizidium Braunii*.

Heterokontae.—*Bumilleria* sp.: *Phlyctidium Bumilleriae*, *Phlyctochytrium biporusum*, *Rhizophydiwm* sp.—*Characiopsis minuta*: *Chytridium Scherffelii*.—*Mischococcus confervicola*: *Rhizophydiwm Mischococci*.—*Ophiocytium arbusculum*: *Rhizophydiwm Sciadii*.—*Tribonema bombycina*: *Chytridium Confervae*, *C. Lagenula*, *Olpidium Sorokinei*, *Plasmophagus Oedogoniiorum*, *Polyphagus parasiticus*, *Rhizophydiwm asterospororum*, *R. goniosporum*, *R. granulosporum*, *R. mammillatum*, *R. (?) persimilis*.—*T. bombycina* var. *minor*: *Rhizophydiwm asymmetricum*.—*Tribonema (?)* sp.: *Olpidium algarum*.

Chrysophyceae.—*Chrysopyxis* sp.: *Rhizophydiwm Chrysopyxidis*.—"Chrysomonad" (cyst): *Rhizophydiwm utriculus*.

Bacillarieae.—*Amphora ovalis*: *Lagenidium enecans*, *Physorhizophidium pachydermum*.—*Amphora* sp.: *Podochytrium clavatum*.—*Asterionella gracillima*: *Rhizophydiwm Schroeteri*.—*Cocconema lanceolatum*: *Lagenidium enecans*, *Olpidium Gillii*.—*Cyclotella Chaetoceras*: *Rhizophydiwm Cyclotellae*.—*C. Kutzningiana*: *Lagenidium Cyclotellae*.—*Cyclotella* sp.: *Rhizophydiwm Cyclotellae*.—*Cymatopleura elliptica*: *Rhizophydiwm clinopus*.—*C. solea*: *Chytridium versatile*, *Lagenidium enecans*, *Rhizophydiwm clinopus*.—*Cymbella cymbiformis* var. *parva*: *Lagenidium brachystomum*.—*C. gastroides*: *Aphanomyopsis Bacillariacearum*, *Lagenidium enecans*.—*Cymbella* sp.: *Rhizophydiwm clinopus*, *R. fusus*.—*Epithemia turgida*: *Aphanomyopsis Bacillariacearum*.—*E. zebra*: *Chytridium Epithemiae*, *Rhizophydiwm Epithemiae*.—*Eunotia Amphioxys*: *Rhizophydiwm globosum*.—*Fragellaria* sp.: *Podochytrium clavatum*.—*Gomphonema constrictum*: *Lagenidium brachystomum*, *Rhizophydiwm fusus*.—*G. micropus*: *Ectrogella Gomphonematis*, *Podochytrium clavatum*.—*G. navicella* (stipes): *Chytridium minus*.—*Gomphonema* sp.: *Ectrogella Bacillariacearum*.—*Hantzschia Amphioxys*: *Olpidium Hantzschiae*, *Rhizophydiwm irregulare*.—*Lauderia borealis* (marine): *Olpidium Lauderiae*.—*Licmophora abbreviata*: *Ectrogella perforans*.—*L. Lyngbyei*: *Ectrogella perforans*.—*Licmophora* sp.: *Ectrogella Licmophorae*, *E. perforans*.—*Melosira varians*: *Chytridium appressum*, *C. nodulosum*, *C. versatile*, *Podochytrium clavatum*, *P. lanceolatum*, *Rhizophydiwm fusus*, *R. globosum*.—*Melosira* sp.: *Podochytrium clavatum*, *Rhizophydiwm fusus*, *R. marinum*.—*Meridion circulare*: *Ectrogella Bacillariacearum*.—*Navicula cuspidata*: *Lagenidium enecans*.—*N. cuspidata* var. *ambigua*: *Lagenidium enecans*.—*Navicula* sp.: *Chytridium perniciosum*, *C. versatile*, *Physorhizophidium pachydermum*, *Podochytrium clavatum*, *Rhizophydiwm clinopus*, *R. gibbosum*, *R. globosum*.—*Nitzschia linearis*: *Lagenidium brachy-*

stomum.—*N. sigmoidea*: *Aphanomyopsis Bacillariacearum*, *Olpidium Gillii*, *Rhizophydiun clinopus*.—*Nitzschia* sp.: *Olpidium Gillii*.—*Pinnularia viridis*: *Aphanomyopsis Bacillariacearum*, *Lagenidium enecans*, *Rhizophydiun globosum*.—*Pinnularia* sp.: *Aphanomyopsis Bacillariacearum*, *Ectrogella Bacillariacearum*, *E. monostoma*, *Lagenidium enecans*, *Lagenidium* sp., *Podochytrium clavatum*, *Rhizophydiun fusus*.—"Pinnularians": *Rhizophydiun gibbosum*.—*Pleurosigma attenuatum*: *Olpidium Gillii*.—*Stauroneis Phoenicentron*: *Lagenidium enecans*.—*Striatella unipunctata*: *Ectrogella perforans*.—*Surirella* sp.: *Rhizophydiun fusus*.—*Synedra lunularis*: *Ectrogella Bacillariacearum*.—*S. ulna*: *Ectrogella Bacillariacearum*, *E. monostoma*.—*S. ulna* (?): *Ectrogella perforans*.—*S. ulna*: *Lagenidium brachystomum*.—*Synedra* sp.: *Aphanomyopsis Bacillariacearum*, *Chytridium versatile*, *Ectrogella Bacillariacearum*, *E. monostoma*, *Lagenidium brachystomum*, *Rhizophydiun fusus*, *Septolpidium lineare*.—*Tabellaria fenestrata*: *Phlyctidium Tabellariae*.—*T. flacculosa*: *Podochytrium clavatum*.—*Tabellaria* sp.: *Chytridium nodulosum*, *C. versatile*.—"Diatoms": *Chytridium acuminatum*, *Ectrogella Bacillariacearum*, *Lagenidium enecans*, *Phlyctidium irregulare*, *Podochytrium clavatum*, *Rhizidium Braunii*, *Rhizophlyctis borneensis*, *Rhizophydiun clinopus*, *R. fusus*, *R. globosum*, *R. irregulare*.

Cryptophyceae.—*Chilomonas* sp. (cysts): *Rhizidium vorax*.—*Cryptomonas* sp.: *Pseudosphaerita radiata*.—*Cryptomonas* sp. (cysts): *Rhizophydiun simplex*.

Euglenophyceae.—*Euglena sanguinia*: *Polyphagus Euglenae*.—*E. viridis* (resting cells): *Chytridium Euglenae*.—*E. viridis*: *Polyphagus Euglenae*, *Saccommyses endogenus*, *Sphaerita Dangeardii*.—*Euglena* sp. (cysts): *Chytridium Euglenae*.—*Euglena* sp.: *Olpidium Euglenae*.—*Euglena* sp. (cysts): *Phlyctochytrium Euglenae*.—*Euglena* sp.: *Polyphagus Euglenae*, *P. Euglenae* var. minor, *Pseudosphaerita Euglenae*, *Saccommyses endogenus*.—*Euglena* sp. (cysts): *Scherffeliomyces parasitans*.—*Euglena* sp.: *Sphaerita Dangeardii*.

Dinophyceae.—*Glenodinium cinctum*: *Pseudolpidium Glenodinium*, *Rhizophydiun echinatum*, "R. globosum."

Phaeophyceae.—*Akinetospora* sp.: *Eurychasma Dicksonii*, *Pleotrichelus Olpidium*.—*Chaetopteris plumosa*: *Olpidiopsis Sphaellarum*.—*Chorda filum* (hairs): *Pleotrichelus minutus*.—*Cladostephus spongiosus*: *Olpidiopsis Sphaellarum*.—*Ectocarpus confervoides*: *Eurychasma Dicksonii*, *Pleotrichelus Olpidium*.—*E. Constanciae*: *Eurychasma Dicksonii*.—*E. crinitus*: *Eurychasma Dicksonii*.—*E. granulosus*: *Eurychasma Dicksonii*, *Olpidiopsis Andreei*.—*E. pusillus*: *Eurychasma Dicksonii*.—*E. siliculosus*: *Eurychasma Dicksonii*, *Olpidiopsis Andreei*.—*Ectocarpus* sp.: *Eurychasma Dicksonii*, *Olpidiopsis Andreei*, *Pleotrichelus Olpidium*.—*Furcellaria* sp.: *Pleotrichelus Olpidium*.—*Punctaria* sp.: *Eurychasma Dicksonii*.—*Pylaiella littoralis*: *Chytridium Polysiphoniae*, *Eurychasma Dicksonii*, *Pleotrichelus Olpidium*,

P. Rosenvingii.—*Sphacelaria cirrhosa*: *Olpidiopsis Sphaellarum*.—*S. tribuloides*: *Olpidiopsis Sphaellarum*.—*Stictyosiphon tortilis*: *Eurychasma Dicksonii*.—*Striaria attenuata* (setae): *Chytridium megastomum*.—*S. attenuata*: *Eurychasma Dicksonii*, *Olpidiopsis Andreei*.

Rhodophyceae.—*Antithamnion Plumulae*: *Olpidium Plumulae*.—*Bangia fuscopurpurea*: *Olpidium entosphaericum*.—*Callithamnion corymbosum*: *Petersenia lobata*.—*C. Hookeri*: *Petersenia lobata*.—*C. roseum*: *Petersenia lobata*.—*Callithamnion sp.*: *Chytridium Polysiphoniae*.—*Ceramium acanthonotum* (?): *Eurychasmidium tumefaciens*.—*C. diaphanum*: *Chytridium megastomum*, *Eurychasmidium tumefaciens*, *Pontisma lagenidioides*, *Rhizophyllum discinctum*, *Thraustochytrium proliferum*.—*C. flabelligerum*: *Eurychasmidium tumefaciens*.—*C. fruticulosum*: *Chytridium Polysiphoniae*, *Pontisma lagenidioides*.—*C. rubrum*: *Chytridium Polysiphoniae*, *Eurychasmidium tumefaciens*, *Petersenia pollagaster*, *Pontisma lagenidioides*.—*C. spiniferum*: *Eurychasmidium tumefaciens*.—*C. strictum*: *Chytridium Polysiphoniae*, *Pontisma lagenidioides*.—*Ceramium sp.*: *Chytridium Polysiphoniae*, *Petersenia pollagaster*.—*Codium mucronatum*: *Chytridium codicola*, *Rhizophyllum codicola*.—*Cystoclonium purpurascens*: *Pyrrhosorus marinus*.—*Delessaria sanguinea*: *Chytridium Polysiphoniae*.—*Dumontia filiformis*: *Olpidium Laguncula*.—*Gymnothamnion elegans*: *Petersenia lobata*.—*Halosaccion ramentaceum*: *Eurychasma sacculus*.—*Polysiphonia elongata*: *Pleotrichelus inhabilis*.—*P. fibrillosa*: *Chytridium Polysiphoniae*.—*P. urceolata*: *Chytridium Polysiphoniae*.—*P. violacea*: *Chytridium Polysiphoniae*.—*Polysiphonia sp.*: *Pleotrichelus Olpidium*.—*Rhodymenia palmata*: *Eurychasma sacculus*.—*Seirospora apiculata*: *Petersenia lobata*.—*S. interrupta*: *Petersenia lobata*.—*Spermothamnion Turneri*: *Petersenia lobata*.—“Floridées”: *Eurychasmidium tumefaciens*.

Characeae.—*Chara coronata*: *Catenaria sphaerocarpa*, *Diplophyctis intestina*, *Endochytrium digitatum*, *Hypochytrium catenoides*, *Nephrocytium appendiculatum*, *Rhizophyllum macrosporum*.—*C. delicatula*: *Diplophyctis intestina*, *Nephrocytium appendiculatum*.—*C. fragilis*: *Diplophyctis intestina*.—*C. polycanthum*: *Diplophyctis intestina*.—*Chara sp.*: *Entophyctis helioformis*.—*Lamprothamnus alopercuroides*: *Diplophyctis intestina*.—*Lychnothamnus barbatus*: *Diplophyctis intestina*.—*Nitella flexilis*: *Catenaria sphaerocarpa*, *Chytridium Lagenaria*, *Diplophyctis intestina*, *Endochytrium digitatum*, *Hypochytrium catenoides*, *Nephrocytium appendiculatum*, *Rhizophyllum macrosporum*.—*N. glomerulifera*: *Diplophyctis intestina*.—*N. gracilis*: *Nephrocytium appendiculatum*.—*N. hyalina*: *Nephrocytium stellatum*.—*N. mucronata*: *Diplophyctis intestina*.—*N. tenuissima* (oögonia): *Chytridium olla*.—*N. tenuissima*: *Diplophyctis intestina*, *Entophyctis helioformis*, *Phlyctochytrium catenatum*.—*Nitella sp.*: *Catenaria Anguillulae*, *Entophyctis helioformis*.—“Characeans”:

Apodachlya pyrifera, *Catenaria Anguillulae*, *Diplophlyctis intestina*.—“Characeae” (öögonia): *Entophlyctis Characearum*.

“*Confervae*.”—“*Conferva rhynophila*”: *Chytridium minus*.—“*Confervacées*”: *Achlyogeton entophytum*.—“*Conferves*” (filaments): *Achlyogeton (?) rostratum*.—“*Conferva*”: *Myzocytium proliferum*.—“*Confervacées*”: *Olpidium algarum*, *O. tuba*.—“*Conferva*”: *Rhizophydiwm mammillatum*.—Palmellaceous green alga (cells): *Rhizophlyctis Palmellacearum*.—“Palmellaceans”: *Rhizophydiwm gibbosum*.

Pteridophyte Spores

Aspidium: *Rhizophydiwm subangulosum*.—*Equisetum*: *Rhizophlyctis rosea*.—*Isoetes echinospora* (microspores): *Rhizophydiwm sphaerotheca*.—*I. lacustris* (microspores): *Ligniera Isoetes*, *Rhizophydiwm sphaerotheca*.

Phanerogams

Gymnospermous pollen.—*Abies* sp.: *Rhizophydiwm pollinis-pini*.—*Pinus austriaca*: *Lagenidium pygmaeum*.—*P. koraiensis*: *Olpidium luxurians*.—*P. Laricio*: *Lagenidium pygmaeum*.—*P. Pallasiana*: *Lagenidium pygmaeum*.—*P. ponderosa*: *Olpidium pendulum*.—*P. strobus*: *Lagenidium pygmaeum*.—*P. sylvestris*: *Lagenidium pygmaeum*, *Rhizophydiwm pollinis-pini*.—*Pinus* sp.: *Olpidium luxurians*, *O. pendulum*, *Phlyctidium pollinis-pini*.—*Pinus* sp. (staminate cones): *Physocladia obscura*.—*Pinus* sp.: *Rhizophydiwm monoporum*, *R. pollinis-pini*, *R. sphaerotheca*.—*Pseudotsuga mucronata*: *Rhizophydiwm sphaerotheca*.—*Taxus* sp.: *Olpidium luxurians*.—“Coniferous pollen grains”: *Lagenidium pygmaeum*.—“Gymnospermous pollen”: *Rhizophydiwm sphaerotheca*.

Angiospermous pollen.—*Cannabis* sp.: *Olpidium luxurians*.—*Lilium* sp.: *Olpidium luxurians*.—*Typha* sp.: *Achlyella Flahaultii*, *Chytridium chaetophilum*, *Olpidium luxurians*, *Rhizophydiwm sphaerotheca*.—“Pollen”: *Olpidium luxurians*.—“Angiosperms”: *Rhizophydiwm pollinis-pini*.

Mature plants.—*Anacharis canadensis*: *Chytridium Elodeae*, *Cladochytrium replicatum*, *Megachytrium Westonii*, *Nowakowskia elegans*.—*Callichtriche autumnalis*: *Sorodiscus Callitrichis*.—*C. stagnalis*: *Ligniera Junci*, *Sorodiscus Callitrichis*.—*C. vernale*: *Sorodiscus Callitrichis*.—*Diplanthera Wrightii*: *Plasmodiophora Diplantherae*.—*Hippuris vulgaris*: *Cladochytrium tenuie*.—*Lemna minor*: *Olpidium Lemnae*.—*L. (Spirodela ?) polyrhiza*: *Olpidium Lemnae*.—*L. trisulca*: *Olpidium Lemnae*.—*Potamogeton natans*: *Ligniera Junci*.—*Ranunculus aquatilis*: *Ligniera Junci*.—*R. circinatus*: *Ligniera Junci*.—*Ruppia maritima* var. *rostrata*: *Tetramyxxa parasitica*.—*R. rostellata*: *Tetramyxxa parasitica*.—*Veronica Beccabunga*: *Cystochytrium radicale*, *Ligniera Junci*.

Vegetable Debris (Including Baits of Vegetable Origin)

Twigs.—*Abies* sp.: *Rhipidium interruptum*, *Sapromyces elongatus*.—*Aesculus* sp.: *Monoblepharis macrandra*, *Rhizidium lignicola*.—*Alnus* sp.: *Apodachlya seriata*, *Araiospora spinosa*, *Pythiomorpha Fischeriana*, *Rhipidium americanum*, *R. interruptum*.—*Betula* sp.: *Apodachlya pyrifera*, *Rhipidium interruptum*.—*Chamaecyparis* sp.: *Sapromyces elongatus*.—*Corylus avellana*: *Chytridium xylophilum*.—*Fraxinus* sp.: *Apodachlya punctata*, *A. pyrifera* var. *macrosporangia*, *Araiospora pulchra*, *Monoblepharis macrandra*, *Rhipidium interruptum*, *Sapromyces androgynus*.—*Picea excelsa*: *Apodachlya pyrifera* var. *macrosporangia*, *Sapromyces elongatus*.—*Picea* sp.: *Sapromyces androgynus*, *S. elongatus*.—*Pinus* sp.: *Sapromyces elongatus*.—*Prunus* sp.: *Araiospora streptandra*, *Rhipidium interruptum*.—*Pseudotsuga mucronata*: *Sapromyces elongatus*.—*Quercus* sp.: *Araiospora spinosa*, *Rhipidium americanum*, *Sapromyces elongatus*.—*Salix* sp.: *Araiospora streptandra*.—*Tilia* sp.: *Chytridium xylophilum*.—“Twigs” (floating): *Apodachlya brachynema*, *A. punctata*, *A. pyrifera*, *A. pyrifera* var. *macrosporangia*, *Araiospora coronata*, *A. pulchra*, *A. spinosa*, *Gonapodya prolifera*, *Macrochytrium botrydioides*.—“Twigs” (submerged): *Monoblepharis fasciculata*, *M. insignis*, *M. macrandra*, *M. ovigera*, *M. polymorpha*, *M. regnicens*, *M. sphaerica*.—“Twigs”: *Myrioblepharis paradoxa*, *Pythiogeton ramosum*, *P. utriforme*, *Pythiomorpha gonapodyides*, *P. undulata*, *Rhipidium elongatum*, *R. interruptum*, *R. parthenosporum*, *R. Thaxteri*, *Sapromyces androgynus*, *S. elongatus*.—“Spruce fir”: *Sapromyces elongatus*.—“Wood”: *Tetrachytrium triceps*.

Fruits.—*Apple* (*Pyrus* sp.): *Apodachlya brachynema*, *Mindenella spinospora*, *Rhipidium americanum*, *R. interruptum*, *R. parthenosporum*, *Sapromyces elongatus*.—*Crataegus* sp.: *Apodachlya brachynema*, *Mindenella spinospora*, *Rhipidium americanum*.—*Pears* (submerged): *Macrochytrium botrydioides*.—*Rose*: *Monoblepharis macrandra* var. *laevis*, *Rhipidium americanum*, *R. interruptum*, *Sapromyces elongatus*.—“Fruit”: *Araiospora coronata*, *Gonapodya prolifera*, *Macrochytrium botrydioides*, *Pythiogeton transversum*, *P. utriforme*, *Pythiomorpha gonapodyides*, *P. undulata*, *Rhipidium americanum*, *R. interruptum*, *R. Thaxteri*.

Soft tissues (mostly bait): *Araiospora spinosa*, *Catenaria Anguillulae*, *C. sphaerocarpa*, *Catenochytridium carolinianum*, *Chytridium xylophilum*, *Cladochytrium cornutum*, *C. polystomum*, *C. replicatum*, *Clavochytrium stomophilum*, *C. tenue*, *Endochytrium operculatum*, *Hypochoytrium catenoides*, *Leptomitus lacteus*, *Monoblepharis sphaerica*, *Nephrochytrium aurantium*, *Nowakowskiella elegans*, *N. ramosa*, *Phlyctochytrium planicorne*, *Pythiogeton autossytum*, *P. ramosum*, *P. transversum*, *P. uniforme*, *Pythiomorpha gonapodyides*, *P. Miyabeana*, *P. Oryzae*, *Rhipidium americanum*, *Rhizophlyctis Petersenii*, *R. rosea*, *Rhizophydium macrosporum*,

Sapromyces androgynus, *S. elongatus*, *Septochytrium variabile*, *Tetra-chytrium triceps*.

Fungi

Achlya americana (hyphae): *Woronina asterina*.—*A. apiculata* (oögonia): *Rhizophyllum carpophilum* (?).—*A. conspicua*: *Rhizidiomyces apophysatus*.—*A. conspicua* (oögonia): *Rhizophyllum carpophilum* (?).—*A. dioica*: *Pringsheimiella dioica*.—*A. flagellata*: *Olpidiopsis Achlyae*, *O. fusiformis*, *O. Saprolegniae*.—*A. flagellata* (hyphae): *Olpidiopsis spinosa*.—*A. flagellata*: *Olpidiopsis varians*, *Pringsheimiella dioica*, *Rhizidiomyces apophysatus*.—*A. flagellata* (oögonia): *Rhizophyllum carpophilum*.—*A. flagellata*: *Rozella simulans*.—*A. flagellata* var. *yezoensis*: *Olpidiopsis fusiformis*.—*A. glomerata*: *Octomyxa Achlyae*.—*A. imperfecta*: *Olpidiopsis fusiformis*, *O. Saprolegniae*.—*A. Klebsiana*: *Rhizidiomyces apophysatus*.—*A. leucosperma*: *Olpidiopsis fusiformis*.—*A. polyandra* (hyphae): *Olpidiopsis fusiformis*.—*A. polyandra*: *Olpidiopsis fusiformis*.—*A. polyandra* (oögonia): *Rhizidiomyces apophysatus*.—*A. polyandra*: *Rozella septigena*, *R. simulans*, *Woronina polycystis*.—*A. prolifera*: *Olpidiopsis fusiformis*.—*A. (Saprolegnia ?) prolifera*: *Olpidiopsis Saprolegniae*.—*A. racemosa* (hyphae): *Olpidiopsis fusiformis*.—*A. racemosa*: *Olpidiopsis fusiformis*, *O. incrassata*, *O. Saprolegniae*.—*A. racemosa* (oögonia): *Rhizophyllum carpophilum*.—*A. racemosa*: *Rozella septigena*, *R. simulans*, *Woronina polycystis*.—*Achlya* sp.: *Olpidiopsis fusiformis*, *O. incrassata*, *O. index*, *O. Saprolegniae*, *Petersenia irregulare*, *Pringsheimiella dioica*, *Rhizidiomyces apophysatus*.—*Achlya* sp. (eggs): *Rhizophyllum carpophilum*.—*Achlya* sp. (oöspores): *Rhizophyllum carpophilum*.—*Achlya* sp.: *Rozella simulans*, *Woronina polycystis*.—*Allomyces arbusculus*: *Rozella Allomycis*.—*Aphanomyces laevis*: *Olpidiopsis luxurians*.—*Aphanomyces* sp.: *Olpidiopsis Aphano-mycis*.—*Apodachlya brachynema* (terminal segments): *Rozella Apodyae-brachynematis*.—*Araiopora spinosa* (sporangia): *Rozella Rhipidii-spinosi*.—*Blastocladia Pringsheimii* (sporangia, immature resting spores): *Rozella Blastocladiae*.—*Chytridium Polysiphoniae*: *Rozella marina*.—*Dictyuchus monosporus* (eggs): *Rhizophyllum carpophilum*.—*Gloeo-sporium Theobromae* (mycelium): *Rhizophyllum fungicola*.—*Lagenidium Rabenhorstii*: *Rozella pseudomorpha*.—*Monoblepharis macrandra* (oöspores): *Rhizophyllum carpophilum*.—*M. polymorpha*: *Rozella Mono-blepharidis-polymorphae*.—*Olpidiopsis Saprolegniae* (sporangium): *Rhizophyllum carpophilum* (?).—*Pezizaceae* (ascocarp of a [?] Helotium): *Hypochytrium infestans*.—*Phlyctidium Bumilleriae*: *Phlyctidium anomalous*.—*Pilobolus crystallinus* var. *areolata* (suspensors, gemmae, mycelium): *Pleotrichelus fulgens*.—*P. Kleinii* (mycelium, suspensors, gemmae): *Pleotrichelus fulgens*.—*P. Pirottianus* (bicellular trophocysts): *Pleotrichelus*

Zopfianus.—*Polyphagus Euglena* (prosorangia): *Rozella Polyphagi*.—*Puccinia Airae* (uredospores): *Olpidium Uredinis*.—*P. Rhamni*: *Olpidium Uredinis*.—*P. Violae* (uredospores): *Olpidium Uredinis*.—*Pythium complens* (oöspores): *Rhizophyllum Pythii*.—*P. dictyosporum*: *Pythiella vernalis*.—*P. gracile*: *Pythiella vernalis*.—*P. intermedium*: "Pleolpidium" inflatum, *Pseudolpidium gracile*, *P. Pythii*, *Rozella cucus*.—*P. monospermum*: *Pseudolpidium Pythii*.—*P. Oryzae*: *Pseudolpidium Pythii*.—*P. rostratum*: *Pseudolpidium Pythii*.—*P. vexans*: *Pseudolpidium Pythii*.—*P. (?) vexans*: *Rozella irregularis*.—*Pythium* sp.: *Pseudolpidium Pythii*.—*Rhizophyllum discinctum*: *Pleotrichelus paradoxus*.—*R. goniosporum*: *Rhizophyllum parasitans*.—*Saccomyces* sp. (prosorangia): *Phlyctidium Dangeardii*.—*Saprolegnia asterophora*: *Olpidiopsis Saprolegniae*.—*S. asterophora* (oögonia): *Rhizidiomyces apophysatus*.—*S. dioica*: *Olpidiopsis Saprolegniae*, *Rozella septigena*.—*S. ferox* (hyphae): *Olpidiopsis incrassata*.—*S. ferox*: *Olpidiopsis Saprolegniae*, *O. Saprolegniae* var. *levis*.—*S. ferox* (oögonia): *Rhizidiomyces apophysatus*.—*S. hypogena*: *Olpidiopsis incrassata*.—*S. littoralis*: *Olpidiopsis incrassata*.—*S. monilifera*: *Olpidiopsis Saprolegniae*.—*S. monoica*: *Olpidiopsis incrassata*, *O. Saprolegniae*, *O. Saprolegniae* var. *levis*, *Woronina polycystis*.—*S. spiralis*: *Woronina polycystis*.—*S. Thureti*: *Olpidiopsis incrassata*, *O. Saprolegniae*.—*Saprolegnia* sp.: *Olpidiopsis incrassata*, *O. index*, *O. Saprolegniae*, *Petersenia irregularis*.—"Saprolegnian": *Rhizidiomyces apophysatus*.—*Saprolegnia* sp. (oögonia, oöspores): *Rhizophyllum carpophilum*.—*Saprolegnia* sp. (hyphae): *Rozella septigena*.—*Saprolegnia* sp.: *Rozella septigena*, *Woronina polycystis*.—*Sphaerita endogena*: *Pseudolpidium Sphaeritae*.—*Synchytrium endobioticum* (resting sporangia): *Phlyctochytrium Synchytrii*.

ANIMALS

Protozoa

Amoeba limax: (?) *Sphaerita endogena*.—*A. verrucosa*: *Nucleophaga Amoebae*.—*Arcella* sp.: *Olpidium Arcellae*.—*Diffugia* sp.: *Olpidium* (?) *Diffugiae*.—*Heterophrys dispersa*: (?) *Sphaerita endogena*.—*Leptophrys vorax* (zoocyst): *Olpidium Leptophrydis*, *Rhizophyllum Leptophrydis*.—*Nuclearia simplex*: (?) *Sphaerita endogena*.—*Pseudospora leptoderma* (zoocyst): *Olpidiomorpha Pseudosporae*.—*P. parasitica*: *Olpidium Pseudosporae*.—*Pseudosporopsis Bacillariacearum* (?): *Olpidium Pseudosporae*.—*Trachelomonas teres* var. *glabra* (*Ilorica*): *Sphaerita Trachelomonadis*.—*Vampyrella pendula* (zoocyst): *Chytridium lateoperculatum*.—*Vampyrella* sp. (zoocyst): *Olpidium Vampyrellae*.—*Vampyrella* sp. (cysts): *Rhizophyllum Vampyrellae*.—"Infusoria": *Catenaria Anguillulae*.—"Mondineae" (cysts): *Endochytrium operculatum*.—"Rhizopods": (?) *Sphaerita endogena*.

Rotifers (Eggs and Adults)

Anuraea cochlearis (?): *Pleotrachelus* (?) *rotatoriorum*.—*Philodina roseola* (adults also): *Woronina elegans*.—“Rotifers” (adults also): *Catenaria Anguillulae*.—“Rotifer”: (?) *Endochytrium oophilum*, *Lagenidium oophilum*.—“Rotifers” (adults also): *Myzocytium zoophthorum*.—“Rotifer”: *Olpidium entophytum* var. *intermedium*, *O. gregarium*.—(?) “Rotifer”: *Olpidium macrosporum*.—“Rotifer”: *Rhizophydium gibbosum*.—“Rotifers” (adults only): *Zoophagus insidians*, *Z. tentaculum*.

Anguillulae

Achlyogeton (?) *rostratum*, *Bericium lethale*, *Catenaria Anguillulae*, *Catenaria* sp., *Myzocytium vermicola*, *Olpidium Nematodeae*, *O. zooticum*, *Rhizophydium vermicola*.

Crustacea

Acroperus leucocephalus: *Chytridhaema Cladocerarum*.—*Chydorus sphaericus*: *Blastulidium paedophthorum*.—*Cyclops* sp. (eggs): *Blastulidiopsis Chattoni*.—*Daphnia obtusa*: *Blastulidium paedophthorum*.—“Daphne”: *Lagenidium giganteum*.—*Lynceus* sp.: *Blastulidium paedophthorum*.—*Sinocephalus retulus*: *Blastulidium paedophthorum*, *Chytridhaema Cladocerarum*.—“Crustacea”: *Blastulidium paedophthorum*, *Chytridhaema Cladocerarum*.—“Copepods”: *Lagenidium giganteum*.

Trematodes (Eggs)

Fasciola hepatica: *Catenaria Anguillulae*.—*Gordius* sp.: *Catenaria Anguillulae*.—“Helminth”: *Catenaria Anguillulae*.—“Liver fluke”: *Catenaria* sp.

Arachnids (Eggs)

“Mite”: *Catenaria Anguillulae*, *Catenaria* sp.

Insects (Exuviae)

Chironomidae (midges): *Asterophlyctis sarcoptoides*, *Obelidium mucronatum*, *Rhizidium mycophilum*, *R. ramosum*, *Rhizoclosmatium aurantiacum*, *R. globosum*, *Rhizophlyctis Petersenii*.—*Ephemerida* (May flies): *Asterophlyctis sarcoptoides*, *Rhizidium mycophilum*, *R. ramosum*, *Rhizoclosmatium aurantiacum*, *R. globosum*, *Siphonaria variabilis*.—*Odonata* (Anisoptera—dragonflies): *Rhizoclosmatium aurantiacum*, *R. globosum*, *Rhizophlyctis Petersenii*, *Siphonaria variabilis*.—*Phryganeidae* (caddis flies): *Asterophlyctis*

tis sarcoptoides, *Obelidium mucronatum*, *Rhizidium ramosum*, *Rhizoclos-matium aurantiacum*, *R. globosum*, *Siphonaria variabilis*.

Ascidians

Anurella: *Nephromyces Roscovitanus*.—*Ctenicella appendiculata*: *Nephromyces* sp.—*Listhephrya*: *Nephromyces Sorokini*.—*Molgula socialis*: *Nephromyces Molgularum*.

Miscellaneous Animal Parts

Apodachlyta brachynema, *A. completa*, *Apodachlyella completa*, *Blastulidium paedophthorum*, *Catenaria Anguillulae*, "Cladochytria" (fossil), *Lagenidium giganteum*, *Monoblepharis polymorpha*, *M. sphaerica*, *Obelidium mucronatum*, *Rhizophyllum macrosporum*, *Tetrachytrium triceps*, *Zygo-chytrium aurantiacum*.

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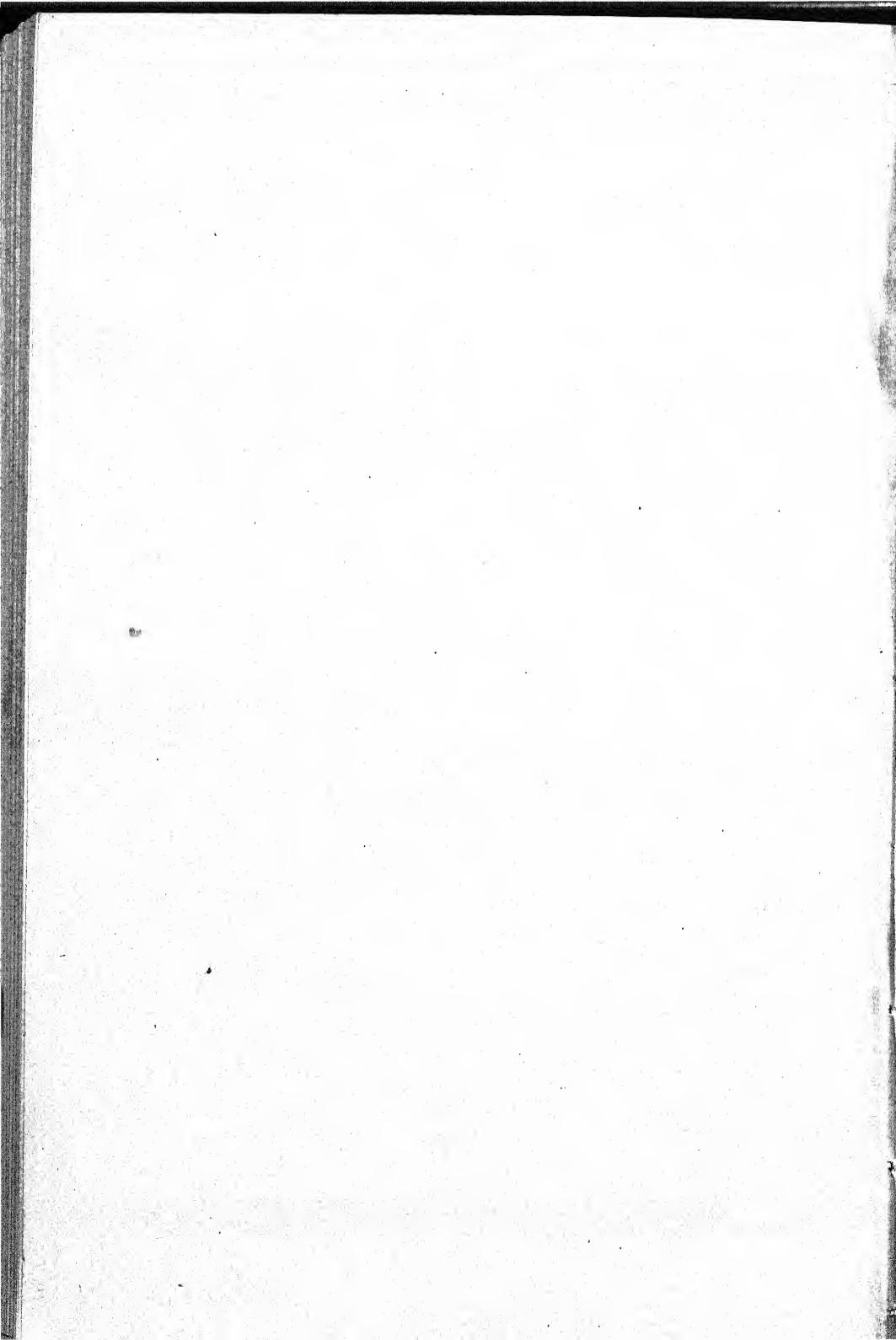
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